UNIVERSITY OF CALIFORNIA,
IRVINE

Drivers of Marine Biodiversity Along a Latitudinal Gradient

DISSERTATION

submitted in partial satisfaction of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

in Ecology and Evolutionary Biology

by

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[2] Wallingford, P.D.*, Pandori, L.L.M.*, Bedgood, S.A., Bracken, M.E.S., **Elsberry, L.A.**, Henry, A.K., Mahanes, S.A. & Sorte, C.J.B. (2018). Seascape Ecology: a guide to the relationships between marine spatial patterns and ecological processes. *Frontiers of Biogeography*. 10, 3-4.

[1] **Elsberry, L.A.**, R.J. Fales, and M.E.S Bracken. 2018. Changes in biodiversity and species associations along a latitudinal gradient. *Frontiers of Biogeography,* 10 (1-2).

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ABSTRACT OF THE DISSERTATION

Drivers of Marine Biodiversity Along a Latitudinal Gradient

By

Laura A. Elsberry

Doctor of Philosophy in Ecology and Evolutionary Biology

University of California, Irvine, 2019

Professor Matthew Bracken, Chair

A major goal of community ecology is to understand how communities are formed and which abiotic and biotic conditions constrain biodiversity and community assembly. To accurately predict and understand how communities are likely to change in response to changes in environmental conditions, it is important to understand the associations between species, the geographic patterns of species associations, how changes in associations and interactions affect community structure, and the demographic characteristics of populations throughout a species' geographic range. To determine if the geographic distribution of species affects site diversity and potential interactions at each site, I executed an observational study of eight sites along the California coast where I categorized species as either narrow-range endemics or widespread species. I found that species were more likely to co-occur with one another south of Point Conception than north of Point Conception indicating potentially positive interactions in a more thermally stressful environment. I also found that narrow-range endemic species were the major drivers of the latitudinal patterns (Chapter 1). To determine if the effect of rockweeds on mobile invertebrate diversity and abundance differed across latitudes and at sites with differing levels of seaweed diversity, I used field observations and experimental removals of two rockweed species at three sites along the California coast. I found that rockweeds tended to increase mobile

invertebrate species richness and abundance, especially at sites where functional redundancy was low (Chapter 2). Lastly, I followed populations of rockweeds at four different sites and characterized growth, survival, and reproduction of individuals over a 12-month period to determine how population demographic patterns differed between leading and trailing edge populations. Using these data, I constructed an integral projection model of each population of rockweeds. I found that populations living in the leading edge and central part of their species' range had similar demographic characteristics, while trailing edge populations had lower population growth estimates and fecundity estimates compared to central populations (Chapter 3). My results identify and highlight some of the important drivers of biodiversity along California rocky shores, especially with respect to changes across spatial gradients and species' ranges.

INTRODUCTION

Global biodiversity is currently threatened by a variety of stressors, including climate change (Pecl et al. 2017). As environmental conditions continue to change, species are faced with limited response options: relocate, adapt to the new conditions, or go locally extinct (Bellard et al. 2012, Singer et al. 2013, Kadowaki et al. 2016). Multiple studies have found that biodiversity declines have increased in the last century due to human impacts (Barnosky et al. 2011, Ceballos et al. 2015), and these declines in biodiversity are likely to alter the functioning of ecosystems (Naeem et al. 2012). It is therefore essential to understand how global change is likely to impact biodiversity so that researchers and policy makers can make better decisions regarding conservation and restoration of ecosystems, habitats, and species (Bellard et al. 2012).

Not all species are likely to respond to global changes in the same way. For example, cosmopolitan species, with broad biogeographic distributions and tolerances to a wide variety of environmental conditions, might be less susceptible to the effects of climate change. However, endemic species – those with narrower biogeographic distributions – tend to have limited geographic ranges because of their restricted physiological tolerances to abiotic conditions (Malcolm et al 2006). These attributes of endemic species make local extinctions and range shifts more likely (Malcolm et al. 2006). As temperatures continue to rise, endemic species have been declining in abundance, causing changes in community assembly and structure (Malcolm et al. 2006). Diversity losses can potentially have strong cascading effects within the ecosystem, causing shifts in species interactions along latitudinal gradients (Travis 1996, Leonard 2000, Pennings & Silliman, 2005, Freestone et al. 2010, Freestone & Osman 2011). It essential to understand the relationships between species' distributions, interactions, and susceptibility to

loss in order to predict species- and community-level responses to global change (Sorte 2013, Maguire et al. 2015).

The field of biogeography – which considers processes operating across species ranges and the potential for distributional shifts – provides essential perspectives for understanding the functional consequences of biodiversity changes. The California coast is an ideal location for evaluating links between marine biodiversity, biogeography, and global change, as the coastline is divided into two major biogeographic provinces. Point Conception divides the California shoreline into cold, nutrient rich waters to the north and warm, nutrient deplete waters to the south (Hohenlohe 2004, Sotka et al. 2004). Point Conception is also a major barrier for dispersal of marine organisms. Some species ranges cross this biogeographic boundary, whereas others end at the point (Newman 1979, Morris et al. 1980, Murray & Littler 1981, Abbott & Hollenberg 1992, Blanchette et al. 2008). Cosmopolitan species with ranges that span Pt. Conception are potentially more tolerant of changing conditions. Endemic species with ranges that end at Pt. Conception may be more susceptible to climate-mediated range shifts.

Once important species associations have been identified, field manipulations can be used to further elucidate the interactions between the two species with differing distributions. Understanding the sign and magnitude of these interactions can help researchers make more specific predictions about how communities and ecosystem functions will respond to a changing environment. One of the major ways that communities are changing is through the loss of foundation species, organisms that provide physical structure and habitat for other species (Ellison et al. 2005). The interactions of foundation species with one another and their associated species are important to understand because of the cascading effects the loss of these foundation species can have on ecosystem functioning (Ellison 2019).

Understanding the demographic characteristics of important species can help lead to conservation efforts that target the most vulnerable stage of an organism. For example, Pandori and Sorte (2019) found that younger life history stages of marine invertebrates are more sensitive to increased warming than older stages. Furthermore, it is important to understand how populations of a species within its geographic range differ in their demographic characteristics to identify important locations to target for conservation. It has been long hypothesized that individuals at the central part of a species' geographic range will out perform individuals at the range edges (Lesica & Allendorf 1995). However, evidence is to support this hypothesis is not consitently found across ecosystems (Sagarin and Gaines 2002).

Identifying species interactions that are important for community assembly and the maintenance of biodiversity can provide important insights into how rocky intertidal communities will respond to global change. The goal of this dissertation research was to evaluate factors that may be important in driving biodiversity along the California rocky shores. I used a combination of observational and experimental studies to address the following questions: 1) How do species association differ across a latitudinal gradient and do these associations differ between widespread and narrow-range endemic species? 2) How does the presence of foundational rockweed species influence the diversity of associated mobile invertebrate species along a latitudinal gradient? 3) Do the demographic characteristics of trailing versus leading edges of rockweeds populations differ; making one edge more susceptible to extinction?

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CHAPTER 1

Changes in biodiversity and species associations along a latitudinal gradient

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Abstract

Biodiversity is currently threatened at local, regional, and global scales, and identifying the species that are vulnerable to these changes is essential for conservation efforts. For example, the breadth of species' ranges may offer important clues to their susceptibility to loss, as widespread species may be more resistant to loss than species with a narrower range breadth. To determine the potential for shifts in community interactions along the latitudinal geographic ranges of species, we examined pair-wise associations between narrow-range endemic and widespread rocky intertidal species. We surveyed rocky intertidal species composition at eight sites along the California coast from San Diego to Cape Mendocino. Four sites were south of Point Conception, and four sites were north of Point Conception. Point Conception is a major biogeographic feature for coastal marine species, where sea surface temperatures transition from cool temperate waters in the north to warm temperate waters in the south. To determine whether pair-wise species associations were significant, we compared the observed communities' standardized effect size to a null model to determine which species occurred together more or less often than by chance. Across all sites, widespread species were considerably more abundant than narrow-range endemic species, and the majority of species were widespread. However, total species richness was unrelated to the number of widespread species, and was, instead, determined by the number of narrow-range endemic species present at a site. Our analyses suggest that species are more aggregated than segregated south of Point Conception, but the opposite is true north of Point Conception. Additionally, we found that species associations between narrow-range endemics drove the overall patterns in species associations. One possible explanation for these patterns is that positive interactions, especially those involving narrow-

range endemic species, are more important in southern California's more thermally stressful intertidal habitats.

Introduction

Global biodiversity is currently threatened by a variety of stressors, including climate change (Pecl et al. 2017). As environmental conditions continue to change, species are faced with limited response options: undergo a geographic range shift, adapt to the new conditions, increase use of facilitative habitats, or go locally extinct (Bellard et al. 2012, Singer et al. 2013, Kadowaki et al. 2016, Jurgens and Gaylord 2018). Biodiversity declines have increased in the last century due to strong human impacts (Barnosky et al. 2011, Ceballos et al. 2015), and these declines are likely to alter the functioning of ecosystems (Naeem et al. 2012). It is essential to understand the potential for global change to impact biodiversity so that better decisions can be made regarding conservation and restoration of ecosystems, habitats, and species (Bellard et al. 2012).

Not all species are likely to respond to global changes in the same way. For example, widespread species, with broad biogeographic distributions and tolerances to a wide variety of environmental conditions, might be less susceptible to the effects of climate change. In contrast, narrow-range endemic species tend to have limited geographic ranges because of their restricted physiological tolerances to abiotic conditions, recent evolutionary history, or dispersal barriers. These attributes of narrow-range endemic species make local extinctions and range shifts more likely (Malcolm et al. 2006). As temperatures continue to rise, some narrow-range endemic species, such as vertebrate and plant species, have been declining in abundance, causing shifts in community assembly and structure (Malcolm et al. 2006). These losses can potentially have

strong cascading effects within the ecosystem, causing shifts in species interactions along latitudinal gradients (Travis 1996, Leonard 2000, Pennings and Silliman, 2005, Freestone et al. 2010, Freestone and Osman 2011). It is essential to understand the relationships between species' distributions, interactions, and susceptibility to loss in order to predict species- and community-level responses to global change (Sorte 2013, Maguire et al. 2015).

Interactions between species can change along latitudinal gradients because of changes in environmental conditions (Leonard 2000, Freestone and Osman 2011). For example, a negative interaction under benign conditions may shift to a facilitative interaction when the interacting species live in a harsh environment. Leonard (2000) found that the canopy-forming seaweed *Ascophyllum nodosum* increased the survival of barnacle recruits south of Cape Cod, Massachusetts, where temperatures were high. However, this facilitative effect disappeared at cooler northern sites. Climate change is also likely to change species' interactions because of differences in the responses of individual species. Sorte et al. (2010) found that many species have undergone poleward range shifts, but the speed of these shifts differs among species. At more local scales, an increase in temperature can lead to a change in the competitive abilities of species, resulting in a shift in the dominant species in a community (Sorte and White 2013). For these marine species, the exposure to warmer air and water temperatures can have strong impacts on species dispersal, development, and stress tolerance. Kelly and Eernisse (2007) found that larval development is faster at warmer locations within a species range, leading to reduced dispersal of those genotypes. Additionally, the expression of heat-shock proteins has also been shown to differ across a species range with higher expression at the range edge than at the center of the distribution (e.g., Sorte and Hoffman 2004).

Many studies have experimentally examined how variation in biodiversity will respond to simulated warming to try to understand how species interactions will change in the future (e.g., Sorte et al. 2010, Gruner et al. 2017). However, observational data can also help us to understand the current state of species interactions. Understanding how species associate with one another and interact can help identify how species losses could impact the community as a whole. If a species is susceptible to extinction (e.g., because of its limited tolerance to changing environmental conditions) then extinction of that vulnerable species may have a cascading effect on other species that it associates and interacts with in an ecological community. One method used to better understand community dynamics is to examine species co-occurrences, a pairwise approach to assess species associations. A species association can be defined as aggregated, segregated, or neutral. A species association is aggregated when species co-occur together more often than expected by chance. An association is segregated when species occur together less often than expected by chance. A neutral association occurs when species co-occurrence cannot be defined as segregated or aggregated (Puri et al. 2014). In this study, we apply this technique to evaluate whether there are regional differences in species associations on opposite sides of a biogeographic boundary, with a particular focus on whether narrow-range endemic and widespread species differ in their associations. Together, narrow-range endemic and widespread species are assembled into communities, but these communities change with latitude, and especially across biogeographic boundaries.

Our research aimed to determine how species associations vary across a latitudinal gradient and how species associations among narrow-range endemics and widespread species differ on along that gradient. We hypothesized that (1) variation in diversity patterns would be primarily associated with widespread species because widespread species are more likely to be

present at many sites; (2) narrow-range endemic species' associations would differ from those of widespread species because widespread species are able to tolerate a wide range of physiological conditions and may not require as many facilitative interactions as narrow-range species; and (3) species associations would change with latitude, with more aggregated species at southern latitudes due to higher thermal and desiccation stresses. We predicted that narrow-range endemic species would exhibit more aggregated associations due to co-evolved relationships with other narrow-range endemic species. Additionally, we predicted that associations would differ regionally and latitudinally due to changes in abiotic conditions.

Methods

Study system

We studied the species living on California, USA, rocky intertidal shorelines (see Supporting Information, Table S1, for species list). The California coast can be divided into two biogeographic provinces, the Oregonian and the Californian, which are separated by Point Conception, a major biogeographic feature for coastal marine species on the California coast. At Point Conception, water temperatures transition from cool temperate waters in the north to warm temperate waters in the south, and larval dispersal is limited (Dawson 2001, Hohenlohe 2004, Sotka et al. 2004, Figure 1.1). Many intertidal species ranges begin or end near Point Conception. To the north, the Oregonian province extends from Point Conception to Dixon Entrance at the border between Alaska (USA) and British Columbia (Canada). To the south, the Californian province extends from Point Conception to Punta Eugenia in Baja California (Mexico) (Valentine 1966, Blanchette et al. 2008).

We grouped rocky intertidal species on the California coast based on whether their ranges crossed the biogeographic boundary at Point Conception. We defined widespread species as those that had geographic ranges that spanned Point Conception. For example, the range of the California mussel, *Mytilus californianus*, extends from the Aleutian Islands in Alaska to Baja California, spanning Point Conception, as well as other biogeographic boundaries (Morris et al. 1980). In contrast, we defined narrow-range endemic species as those with narrow biogeographic ranges that did not extend Point Conception. For example, the brown seaweed *Fucus gardneri* ranges from Washington to Point Conception, and its range does not cross a major biogeographic boundary (Abbott and Hollenberg 1992). These species are typically adapted to a more limited range of abiotic conditions; species at higher latitudes are typically more adapted to cooler conditions, whereas species at lower latitudes are usually adapted to warmer temperatures.

Study sites

We performed a latitudinal survey of sites spanning 1,044 km of the California rocky shoreline between March and September of 2015. We surveyed eight sites, ranging from Cape Mendocino in northern California to Scripps Reserve in southern California: Cape Mendocino (CM; 40.34° N, 124.36° W), Bodega Bay (BB; 38.32° N, 123.07° W), Big Creek (BC; 36.07° N, 121.61° W), Cambria (CAM; 35.56° N, 121.08° W), Coal Oil Point (COP; 34.41° N, 119.88° W), Point Fermin (PF; 33.71° N, 118.29° W), Crystal Cove (CC; 33.58° N, 117.84° W), and Scripps (SCR; 32.88° N, 117.26° W; Fig. 1). Four of our sites were north and west of the biogeographic boundary at Point Conception (34.45° N, 120.40° W), and four were south and east of Point Conception.

Survey methods

At each site, we laid down 10 transects perpendicular to the water line. We surveyed species composition in a 0.25 m^2 quadrat positioned every vertical 0.5 m on each transect, starting at the mean lower-low water level. Sampling effort varied due to site topography, with quadrats sampled at each site ranging from 14 to 40 as follows: CM = 33, BB = 40, BC = 33, CAM = 30, COP = 14, PF = 24, CC = 25, SCR = 30. Locations at each site were chosen haphazardly based on where a 50 m transect could be placed parallel to the water's edge. Most sites were relatively consistent in the number of quadrats sampled. We estimated the percent cover of sessile invertebrates and algae using 100 evenly spaced grid points. All mobile invertebrates were counted within each quadrat. In most cases, we were able to identify organisms to species in the field. When species were identified only to a higher taxonomic level (e.g., genus), then we determined the possible species that could have been present and assigned the appropriate distribution based on all possible species within that group. For example, *Phyllospadix* spp. was identified as widespread because both *P. torreyi* and *P. scouleri* are found from Canada to Baja California (Phillips and Meñez 1988).

Statistical analyses

To examine community associations between species, we calculated standardized effect sizes (SES) of pair-wise species associations (Sfenthourakis et al. 2006). A SES score is a comparison of mean co-occurrence of species pairs to a null model. We defined a SES value as significant if it was at least one standard deviation (± 1.96) from the mean. SES values are calculated from presence-absence matrices, so we converted our abundance and percent cover data into presence-absence. Simulations and analyses were conducted in R using the community

ecology package, vegan (version 2.3-2). We calculated SES values for every species pair on each transect (n = 10) at each site. The number of significant associations was normalized by the number of possible associations at each site. Most associations were not significant; therefore, the percentage of significant associations was small, ranging from 0.1 to 4.1% (Table 1.1). We identified a total of 86 taxa in our surveys, which corresponds to a total of 3,655 (= $[86^2 - 86]/2$) potential pairwise interactions if every species were able to interact with every other species. Approximately 5% of all possible species pairs, or 183 pairs, could be expected to show a deviating association by chance. However, the total number of observed significant pairwise associations (206) was greater than 183 (Table 1.1).

To determine how latitude influenced species associations, we used linear regression to determine the effect of latitude on the number of significant species associations, the number of significant associations between narrow-range endemic and widespread species, and the number of significant associations between widespread species. We also used t-tests to determine whether there were regional differences in aggregations and segregations.

Results

Species abundance and richness

Our surveys identified an average (±SEM) of 25 (± 1) widespread species and 10 (± 2) narrow-range endemic species at each site (Figure 1.2). Most of the species at each site were widespread, except at Cambria where the species richness was split evenly between widespread and narrow-range endemic species (Figure 1.3a). Across all sites, narrow-range endemic species were significantly lower in abundance than widespread species (Figure 1.3b). At the three most

northern sites (Big Creek, Bodega Bay, and Cape Mendocino), relative narrow-range endemic species abundance was only 2 to 8% (Figure 1.3b).

However, total species richness at sites was unrelated to the number of widespread species at those sites (Linear Regression, $R^2 < 0.01$, $p = 0.901$; Figure 1.4a). Instead, total species richness was most strongly associated with narrow-range endemic species richness (Figure 1.4b; Linear Regression, $R^2 = 0.78$, $p = 0.003$). Cambria was the most diverse location, with 42 species, likely associated with its proximity to Point Conception. Big Creek had the lowest overall species richness with only 28 species. There were more narrow-range endemic species in southern California (i.e., south of Point Conception) than in northern California; 17 southern narrow-range endemic species and 10 northern narrow-range endemic species were present in our surveys.

Species associations

When all significant species associations were considered, we found that the total normalized number of associations was not related to latitude (Linear Regression: $R^2 = 0.18$, $F_{1,6} = 2.58$, $p = 0.185$; Figure 1.5a). However, as latitude increased, the number of narrow-range endemic pair-wise species associations decreased (Linear Regression, $R^2 = 0.48$, $F_{1,6} = 7.43$, $p = 0.034$; Figure 1.5b). Similarly, the number of significant associations between narrow-range endemic and widespread species tended to decrease with increasing latitude (Linear Regression, $R^2 = 0.38$, $F_{1,6} = 5.27$, $p = 0.061$; Figure 1.5c). However, there was no relationship between the number of significant associations and latitude when only associations between widespread species were considered (Linear Regression, $R^2 = 0.17$, $F_{1,6} = 0.00$, $p = 0.980$; Figure 1.5d).

Species aggregations were more common south of Point Conception than north of Point Conception regardless of the type of species included in the analysis (Figure 1.6). When all species associations were included, there was no difference between the two regions ($t = 2.01$, df = 3.86, $p = 0.117$). However, when only associations between narrow-range endemic species were included in the analysis, the difference between aggregated and segregated associations in the south was higher than the difference in the north ($t = 5.65$, df = 6, $p = 0.001$). When widespread species were included (either widespread-widespread associations or associations between widespread and narrow-range endemic species) there was no difference between sites south and north of Point Conception (widespread-widespread: $t = 1.0$, df = 3.16, $p = 0.388$; narrow-range endemic-widespread: $t = 1.1$, df = 4.42, $p = 0.348$).

Discussion

We had hypothesized that widespread species would drive patterns of abundance. This hypothesis was supported: widespread species were universally the most abundant species at our study sites (Figs. 2, 3), and they represented the majority of species across all sites (Fig. 3). We also hypothesized that widespread species would drive patterns of diversity. However, the number of species at a location was actually most strongly related to narrow-range endemic species richness; widespread richness was unrelated to total species richness (Fig. 4). Furthermore, even though narrow-range endemic species were not highly abundant, they were involved in an unexpectedly large proportion of significant associations, indicating that, despite their low abundances, narrow-range endemic species may be disproportionately important in determining community structure (Bracken and Low 2012, Mouillot et al. 2013).

The number of significant species associations tended to decrease with latitude for all species pairs except widespread pairs (Fig. 5). This trend was only statistically significant for narrow-range endemic species pairs, which could be associated with two phenomena. First, slightly fewer narrow-range endemic species were present at sites north of Point Conception. Second, species interactions – which can underlie associations – can change with latitude. For example, Freestone and Osman (2011) found that communities at lower latitudes were more influenced by local interactions with narrow-range endemic species and those at higher latitudes were influenced by widespread species. Leonard (2000) showed that interactions between the canopy-forming seaweed *Ascophyllum nodosum* and barnacles changed from negative to positive at southern sites where temperatures were higher. The relationship between species associations and latitude – particularly for narrow-range endemic species – suggests that these associations may be altered under future climatic conditions.

Regionally, we observed more aggregated associations in the south and more segregated associations in the north (Fig. 6). Since aggregated associations can be indicative of positive interactions, more aggregations in the south could indicate that positive interactions are more common in the more thermally stressful environment of southern California. However, aggregated associations may also indicate positive density dependence between a consumer and its resources. Therefore, these associations need to be examined on a case-by-case basis to identify the nature of the interaction between the species. These regional differences could also be due to differences in the vertical extent of the intertidal zone. Northern sites were generally characterized by broader intertidal ranges, despite similar tidal amplitudes, likely due to larger waves on the more exposed coasts north of Point Conception. With more vertical space in the intertidal zone, there is more potential for segregation.

We can use the observed associations between species pairs to infer the nature of the relationship between the two species. For example, we found that the widespread species *Mytilus californianus* (California mussel) and *Pollicipes polymerus* (gooseneck barnacle) were aggregated together more often than by chance, likely because they share a similar niche in the intertidal zone. Two chitons, *Nuttallina fluxa* and *Cyanoplax hartwegii* are narrow-range endemic species in the Californian province, and we found that they were segregated more often than by chance. *Nuttallina* typically lives higher on the shore and is more commonly found on bare rock. In contrast, *Cyanoplax* is found at intermediate tidal elevations and almost exclusively under canopies formed by the brown seaweed *Silvetia compressa*. Additionally, these two species compete for the same food source: crustose seaweeds and microalgae. This association pattern may be driven by competition for food or by physiological tolerance differences between these two species. However, the relationship between *Silvetia* and *Cyanoplax* is an example of an aggregation associated with stress amelioration; removal of the *Silvetia* canopy results in declines in *Cyanoplax* (Sapper and Murray 2003). This relationship is representative of species aggregations that are more common in southern California because of the harsher abiotic conditions associated with this region (Schoch et al. 2006).

Endemic species are a focus for conservation because they increase overall diversity and maintain community structure (Stachowicz et al. 2008). Endemic species are the targets of many conservation efforts across biomes. These species are particularly susceptible to extinctions because of their constrained geographic ranges, and the loss of these species may have cascading effects (Malcolm et al. 2005). The number of endemic species has been used to identify "biodiversity hotspots" where conservation efforts and funds should be focused (Myers et al. 2000). Our study shows that narrow-range endemic species may have a strong role in shaping

rocky intertidal communities by influencing variation in diversity patterns along the California coast. Overall, we found that narrow-range endemic species were characterized by different associations compared to widespread species. Species associations changed latitudinally, with more associations south of Point Conception than in the north. Despite their low abundances, narrow-range endemic species were highly influential in these trends, highlighting their importance in rocky shore communities.

As climate change continues to affect species' geographic distributions, narrow-range endemic species may be disproportionately threatened due to their narrow biogeographic ranges and limited tolerances to abiotic conditions. Given that narrow-range endemic species were disproportionately responsible for variation in patterns of both species richness and species associations, climate-mediated shifts in their distributions are likely to alter biodiversity, species associations, and–by extension–ecosystem functioning, including shifts in interactions among species and/or changes in overall community productivity (Leonard 2000, Bracken and Low 2012, Naeem et al. 2012). Understanding how narrow-range endemics are associated with other species in ecological communities can be an important aspect to consider in conservation and management planning to maintain current ecosystem functioning. Linking biogeography, biodiversity, and species associations can help elucidate how current communities are structured and allow better predictions regarding how communities and ecosystems are likely to change in the future (Blonder et al. 2017).

Table 1.1 Number of species associations at each site: total, narrow-narrow, narrow-widespread, and widespread-widespread

Site	Total	Narrow-narrow	Narrow-widesperad	Widespread-widespread
Scripps	496	6	7	6
Crystal Cove	378	2	11	9
Point Fermin	378	2	10	14
Coal Oil Point	861	1	13	37
Cambria	465	1	12	18
Big Creek	595	0	5	14
Bodega	741	0	4	11
Cape Mendocino	595	0	4	19

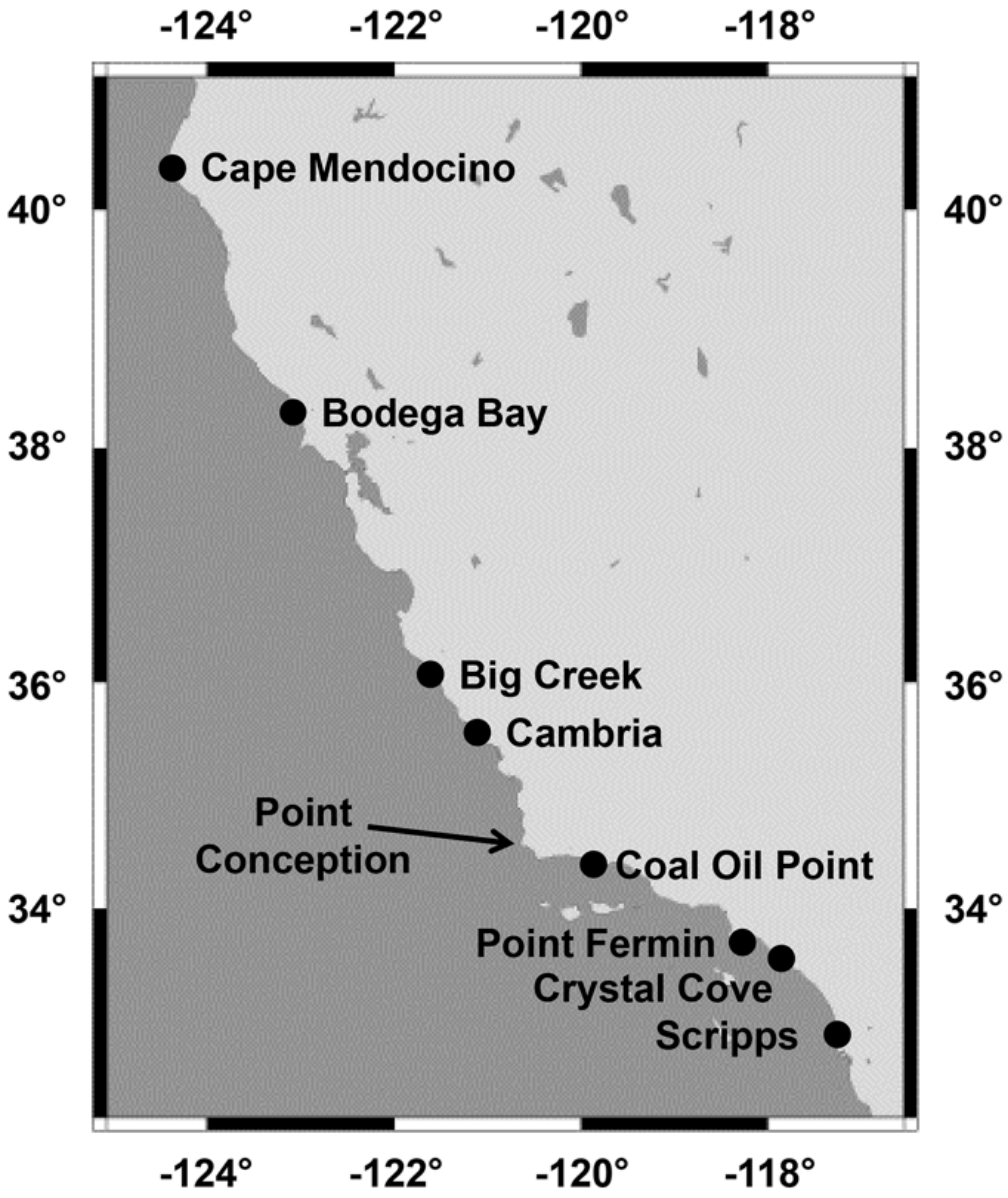

Figure 1.1 Eight study sites spanned the California, USA, rocky shoreline. Cape Mendocino, Bodega Bay, Big Creek, and Cambria are north of Point Conception. Coal Oil Point, Point Fermin, Crystal Cove, and Scripps are south of Point Conception.

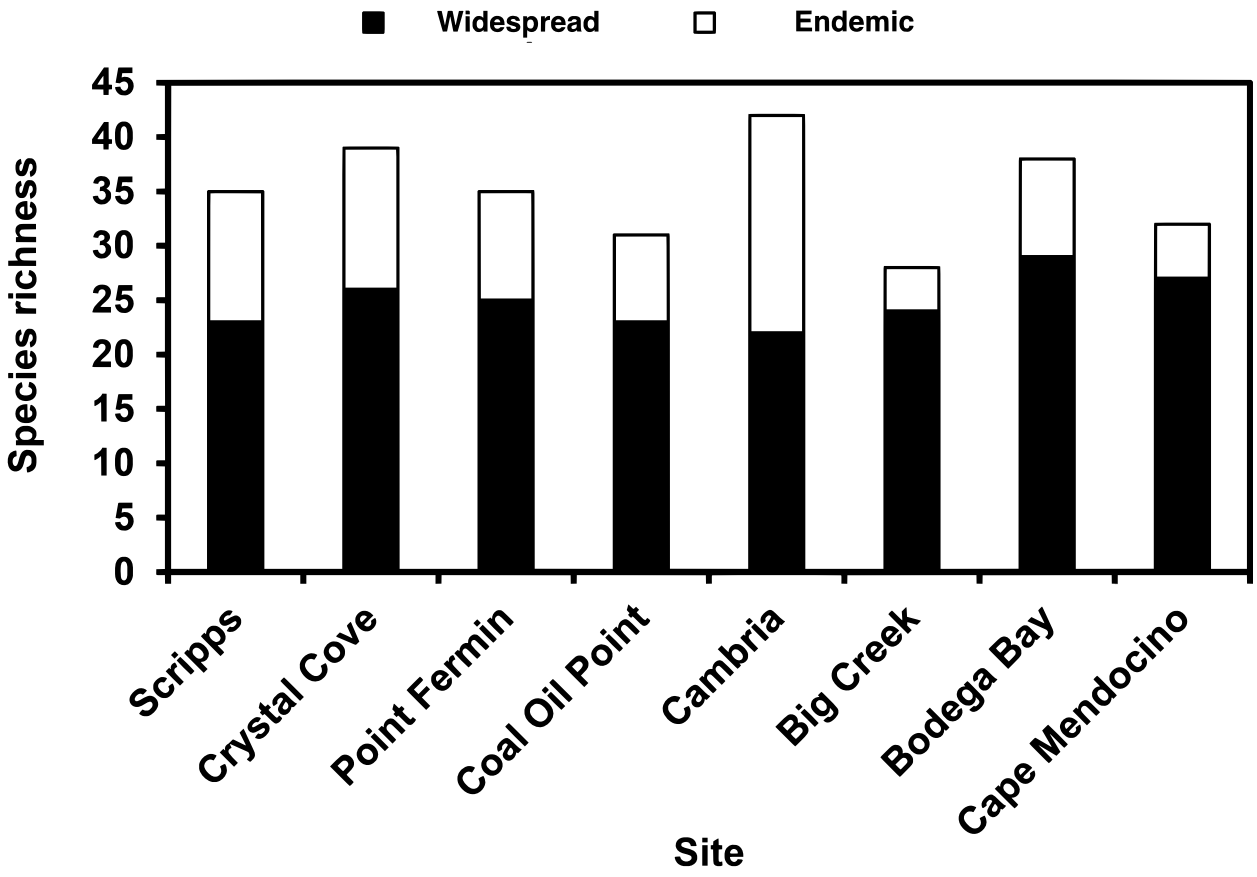

Figure 1.2 Diversity of narrow-range endemic and widespread species. Sites are listed latitudinally from south to north. The average (±SEM) of widespread richness was 25 (±1) species at all sites. Higher species richness (e.g., at Crystal Cove and Cambria) was primarily due to narrow-range endemic species.

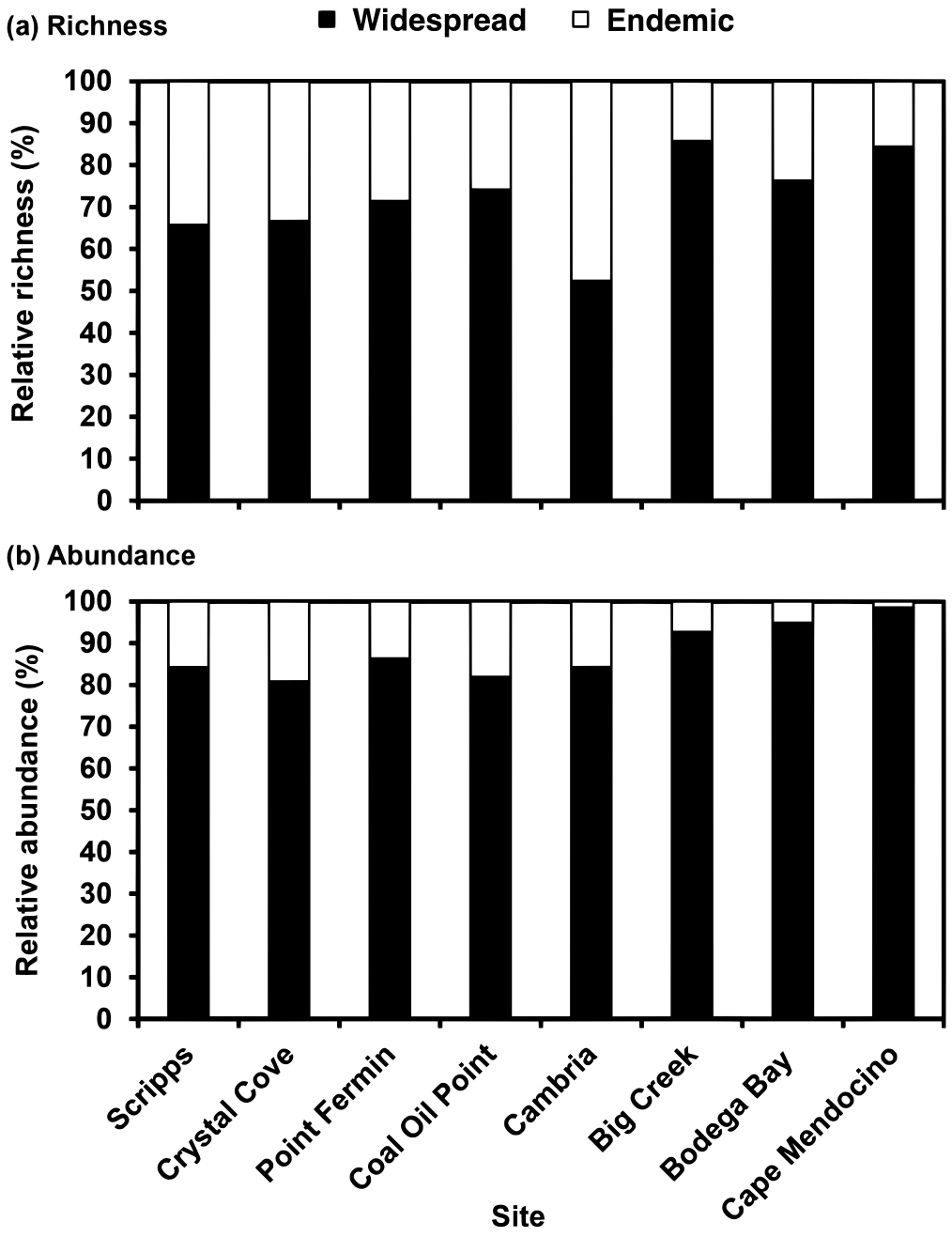

Figure 1.3 Relative species richness and abundance. (a) The majority of species were widespread species; on average, narrow-range endemic richness across sites made up less than 30% of total richness. (b) Narrow-range endemic species made up 20% or less of the total abundance at each site.

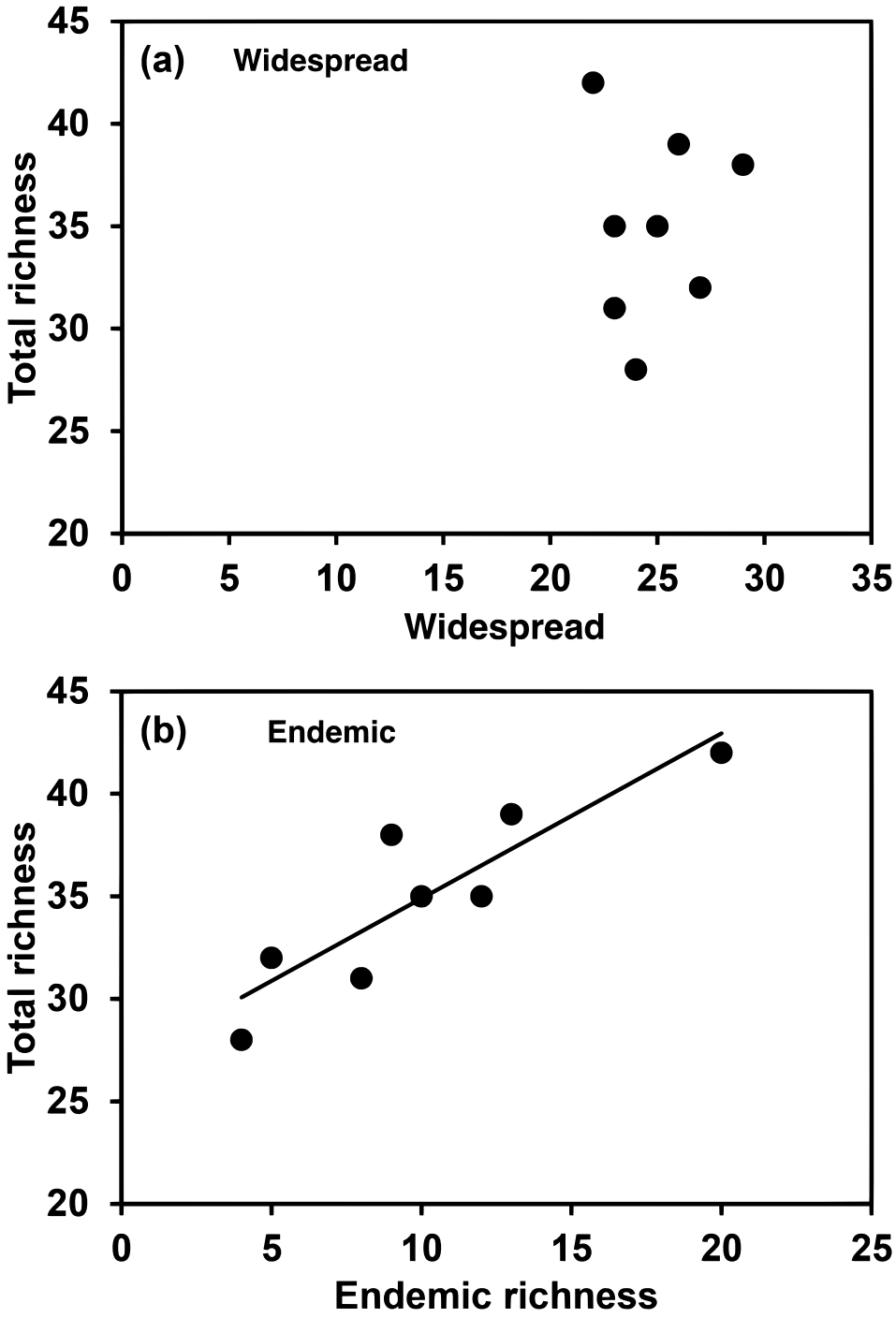

Figure 1.4 Relationship between species richness and the number of (a) widespread species and (b) narrow-range endemic species. Whereas the number of widespread species was unrelated to total species richness (R^2 = 0.00, p = 0.901), the number of narrow-range endemic species at a site was strongly correlated with total species richness (R^2 = 0.78, p = 0.003).

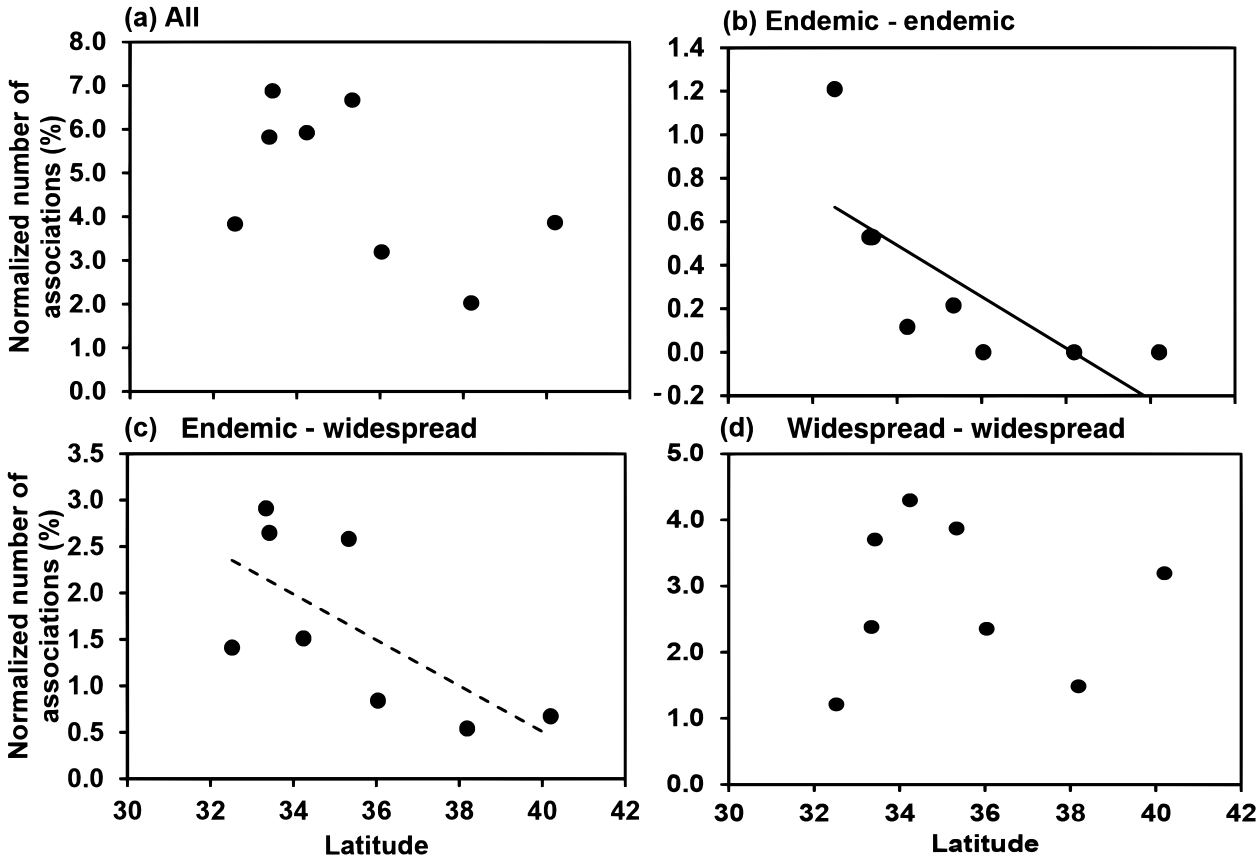

Figure 1.5 Number of species associations normalized by the number of possible associations by latitude: (a) all species associations, (b) associations between narrow-range endemic species, (c) associations between narrow-range endemic and widespread species, and (d) associations between widespread species. The number of associations decreased with increasing latitude when narrow-range endemic species were included (a, b, and c). When only widespread species were included there was no relationship between latitude and species associations.

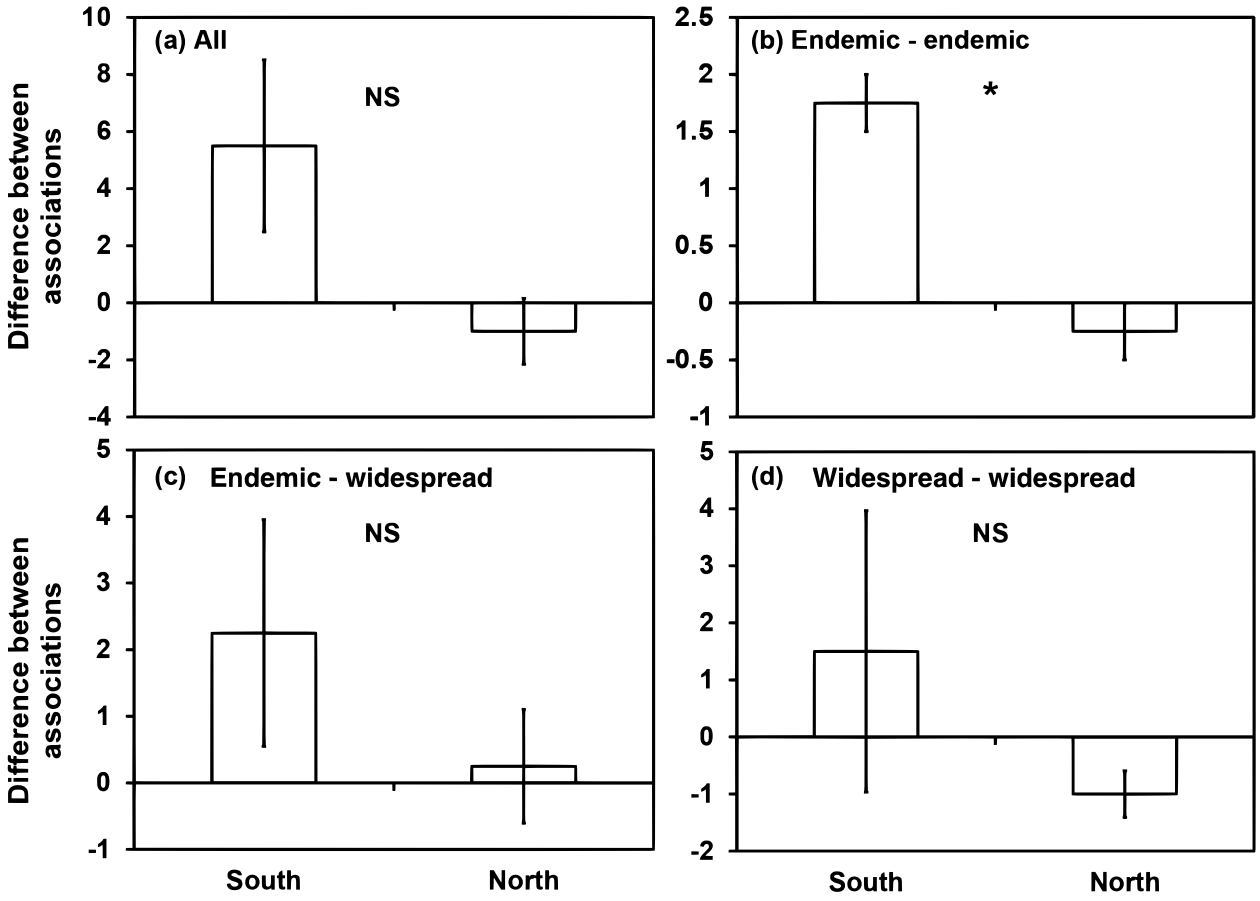

Figure 1.6 Average (±SEM) difference between aggregated and segregated species associations south and north of Point Conception: (a) all species associations, (b) associations between narrow-range endemic species, (c) associations between narrow-range endemic and widespread species, (d) associations between widespread species. In all cases, aggregated associations were more common south of Point Conception than north. (N = 4 sites per region)

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CHAPTER 2

Functional redundancy buffers mobile invertebrates against the loss of foundation species on rocky shores

Abstract

Foundation species are vital to the maintenance of biodiversity and ecosystem functioning in many systems. For example, on rocky shores, rockweeds – large brown algae in the Order Fucales – have the potential to provide habitat and ameliorate stress for mobile invertebrates. To determine the relative role of two rockweeds (*Silvetia compressa* and *Pelvetiopsis* spp.) as foundation species at sites along a latitudinal gradient, we conducted observational surveys and then initiated a 12-month removal experiment. We found that richness and abundance of mobile invertebrates declined over time when rockweeds were removed, but only at the southernmost site. In contrast, at our other sites, there was no change in the richness and abundance of mobile invertebrates following rockweed removal. At the southern site, rockweeds played an important role in maintaining mobile invertebrate diversity. However, at our central and northern sites, rockweeds were less important in maintaining the diversity of mobile invertebrates. At these sites, alternative species – bladed and branching taxa in the genera *Mastocarpus*, *Mazzaella*, *Corallina*, and *Endocladia* – co-occur with rockweeds and can buffer the system against their loss. However, these alternative foundation species are rare to absent at the southern site. The loss of rockweed foundation species, which are declining at our southern site, can have cascading effects by causing co-extinctions of associated species. This study highlights the importance of conserving foundation species, especially in areas where their functional redundancy is low, so that biodiversity and ecosystem functioning can be maintained.

Introduction

Foundation species – dominant species that provide habitat for other organisms (Bracken et al. 2007, Ellison 2019) – play integral roles in maintaining ecosystem function and biodiversity in a multitude of habitats. Foundation species modify the physical structure of ecosystems, influencing the diversity and abundance of associated species (Bertness et al. 1999, Bruno and Bertness 2001). These species can regulate the diversity of associated species by allowing additional species to survive in a location or by reducing the survivorship of competing species (Dayton 1971, Bertness et al. 1999, Lilley and Schiel 2006). The role and importance of a foundation species can vary across locations depending on environmental conditions and presence of other foundation species.

Understanding how foundation species interact with other species and the effects of those interactions has been a long-standing goal of ecologists. Recognizing the importance of direct and indirect relationships between organisms is important for predicting how ecosystems will respond to the threat of climate change. The loss of foundation species has resulted in corresponding rapid declines in biodiversity across habitats, making it increasingly important to understand how these changes will impact systems (Ellison et al. 2005). In the last decade, researchers have highlighted the importance of understanding how species interactions, including those with foundation species may change in response to global climate change (Tylianakis et al. 2008). The complex nature of the interactions of foundation species with the species and ecosystems associated with them is an important aspect of understanding how communities are likely to change (Ellison et al. 2005). For example, the decline of the American chestnut has led to not only changes in the communities directly associated with the chestnut but to changes in adjacent aquatic invertebrate communities (Vandermast et al. 2001).

On southern California rocky shores, the rockweed *Silvetia compressa* provides stress amelioration for the chiton *Cyanoplax hartwegii*, and removal of the *Silvetia* canopy results in declines in *C. hartewegii* (Sapper and Murray 2003). Similarly, removal of the fucoid seaweed *Hormosira banksii* from the New Zealand rocky intertidal zone resulted in profound changes in community structure, including declines in understory algae (Lilley and Schiel 2006). Canopy-forming macroalgae can also have negative effects on other species, including preventing the recruitment of understory species by limiting light or by abrading recruits with their branches (Kiirikki 1996, Connell 2003, Jenkins et al. 2004), but, on average, foundation species tend to enhance the diversity and abundance of associated taxa (Bracken et al. 2007). Because of the roles that foundation species may play in ameliorating stress, understanding how communities are impacted by the loss of these important species can allow researchers to make better predictions about how systems will be altered by climate change. Given their roles in maintaining biodiversity and mitigating stress, foundation species may be important targets for conservation (Bracken et al. 2007).

Whereas many systems, including forests and coral reefs, are maintained by multiple foundation species operating concurrently, there has been limited research investigating how multiple foundation species impact ecosystems (but see Altieri et al. 2007, Angelini et al. 2011). A system that is maintained by multiple, co-occurring foundation species may be characterized by a "faciltation cascade", where one foundation species enhances another. For example, Altieri et al. (2007) found that cordgrass facilitated the settlement of mussels, which further increased the community strucutre and effect of foundation species on New Engand shores. Similarly, Bracken (2018) documented kelp – a known foundation species – growing on tubeworms, which provided a hard substratum in an otherwise unsuitable soft-sediment habitat. It is clear that

multiple, co-occurring foundation species collectively structure many ecosysetms, but most research still focuses on a single, dominant species. We therefore focused on the roles of two important, co-occurring foundation species on California rocky shores.

Furthermore, the interactions between species can vary across locations depending on the biotic and/or abiotic conditions associated with a site. For example, the roles that foundation species play in structuring a community can change from facilitative to inhibitory depending on conditions. Leonard (2000) found that the interactions between *Ascophyllum* and barnacle species in New England differed between northern and southern sites. *Ascophyllum* only played a facilitative role, enhancing barnacle survival, at more thermally stressful southern sites. At northern sites, predator abundances were higher under the algal canopy, and barnacle survival was reduced in the presence of *Ascophyllum* (Leonard 2000). This research highlights the need to understand the context-dependency of the relationships between foundation and associated species.

Foundation species can also compete with one another for primary space and other resources, and the interaction sign and magnitude of each foundation species can differ among species. For example, palo verde trees and saguaro cacti are two co-occurring foundation species in the Sonoran Desert. Palo verde trees provide shade and frost protection, ameliorating stress for small saguaros (Vandermeer 1980). However, the palo verde trees are subsequently out-competed by mature saguaros and are less effective at providing reseources for desert animal species (Turner et al 1966, Wolf and del Rio 2003). The benefit of having multiple foundation species in a system appears to be context dependent. If one foundation species is lost, a community may remain more stable if another species is functionally redundant and can fulfill the same role in the associated communities.

Rockweed species – brown algae in the Order Fucales – can be found on rocky shores worldwide (Benedetti-Cecchi et al. 2001, Sapper and Murray 2003, Lilley and Schiel 2006). Multiple studies have demonstrated that rockweeds are declining, including some cases of local extinction (Benedetti-Cecchi et al. 2001, Gunnill 1980, Jenkins et al. 2008). Along the coast of California, USA, the mid- to upper-intertidal zone is dominated by rockweeds that form dense canopies, potentially providing habitat for a number of species. California rockweeds are also under threat and have been in decline over the past several decades (Whitaker et al. 2010). Declines in these dominant foundation species may have cascading effects on ecosystem functioning and stability (Crowe et al. 2013, Ellison 2019).

Here, we addressed how the roles of multiple rockweed species (*Silvetia compressa*, *Pelvetiopsis limitata*, and *Pelvetiopsis californica*) in structuring mobile invertebrate communities may change along a gradient in environmental conditions along the California coast. We hypothesized that rockweeds would ameliorate harsh physical conditions, increasing the abundance and richness of associated mobile invertebrate species. We also hypothesized that mobile invertebrate assemblages would be negatively impacted by the removal rockweeds at all sites.

Methods

Study sites and species

We conducted surveys and experiments at three sites across ~700 km of the California rocky shoreline between June 2016 and July 2017 (Figure 2.1, Table 2.1). Sites included the University of California Bodega Marine Reserve (38.32° N, 123.07° W), the University of

California Kenneth S. Norris Rancho Marino Natural Reserve (35.56° N, 121.08° W), and Corona del Mar State Beach (33.59° N, 117.87° W).

The geographic distribution of *Silvetia compressa* (J. Agardh) E.Serrão, T. O. Cho, S. M. Boo and Brawley is from Humboldt County, California, USA to Punta Baja, Baja California, Mexico (Silva 1990). *S. compressa* was present at all three of our study sites. The geographic distribution of *Pelvetiopsis limitata* (Setchell) N. L. Gardner is from Vancouver Island, British Columbia, Canada to San Luis Obispo County, California, USA (Abbott and Hollenberg 1976). The geographic distribution of *Pelvetiopsis californica* (P. C. Silva) Neiva, Raimondi, G. A. Pearson and Serrão is from San Luis Obispo County, California, USA to Islas San Benito, Baja California, Mexico (Abbott and Hollenberg 1976). Hereafter, *Pelvetiopsis* refers to *P. limitata* at Bodega Marine Reserve and Rancho Marino and to *P. californica* at Corona del Mar.

Intertidal distributions and physical characteristics of species and sites varied with location (Table 2.1). The maximum tide height of *Silvetia compressa* increased slightly at more northern locations. The minimum tide height of *S. compressa* was similar at Bodega Marine Reserve and Rancho Marino but much lower at Corona del Mar. The tidal distribution of *Pelvetiopsis limitata* was higher at Bodega Marine Reserve than Rancho Marino. Within the *Silvetia* zone, the average air and water temperature at each site increased with decreasing latitude.

Observational study

At our three study sites, we surveyed the rockweed zone (typically low to mid-high intertidal) for the abundance of rockweeds and their associated taxa. At each site, a 50 meter transect was laid parallel to the water line, and 10 vertical transects were randomly placed along

the horizontal transect. Along each vertical transect, we surveyed five 0.25 m^2 evenly spaced quadrats within the zone of each species (N = 50 quadrats / per site). We counted the number of mobile invertebrates in each quadrat and quantified cover of sessile invertebrates and macroalgae. Species were identified to the lowest taxonomic level using field guides and taxonomic keys. Surveys were conducted prior to initiating experiments in June and July 2016.

Removal experiment

Based on the data from our observational study, we determined the center of each rockweed species' vertical distribution based on abundances, and we established N = 15 circular plots (25 cm diameter) at this central elevation for each species at each of our three study sites (Figure 2.1). We selected the center of the distribution to minimize impacts to the upper and lower edges of the populations, where abundances were lower. This was especially important given that two of our study locations were in marine protected areas. At each site, we applied treatments to each rockweed species independently of one another. At each site, we established and maintained N = 3 replicates of each of five treatments: (1) no rockweed (natural absence), (2) rockweed absent but mimic disturbance associated with removal, (3) rockweeds present, (4) rockweeds present and mimic disturbance, and (5) rockweeds removed (press removal). Prior to the application of treatments, all plots were surveyed for abundance of rockweed (cover) and mobile invertebrate species (individual counts). Plots where rockweeds were present had at least 80% cover of the target rockweed species prior to the application of the treatment. For mimicked disturbance treatments, we haphazardly scraped four one-cm-diameter areas (approximately the size of holdfast attachments). For the press removal treatment, we removed the entire thallus of the target rockweed species within the plots. We also trimmed the branches of adjacent rockweed

thalli surrounding the removal plots to prevent impacts of canopy of plants attached outside of the plots. Plots were resurveyed every three months for one year. We removed all rockweed recruits that had grown in the plot on each survey date.

Data analysis

To determine if effective tide height influenced mobile species richness and abundance, we divided the quadrats into five zones (low, low-mid, mid, mid-high, high) based on surveyed tidal elevations. No rockweeds were present in the high zone, so this zone was omitted. For each site, we used a two-way ANOVA to compare the effect of tide height and rockweed presence and species identity on mobile invertebrate richness and abundance. Tukey post-hoc tests were used to compare the effects of rockweed species at each tide height. We used a repeated-measure ANOVA to compare removal and control plots over time at each site. Pair-wise post-hoc tests were done to compare treatments at each time point. Lastly, we compared the mobile invertebrate community pre-removal and 12 months post-removal using PERMANOVA and SIMPER analyses. Analyses were conducted using R ezANOVA and vegan packages (R Core Team 2015).

Results

Observational study

The average percent cover of *S. compressa* was highest in the low-mid zone of the intertidal at each site (Figure 2.1B, 2.1C, and 2.1D). *P. limitata* was present at the Bodega Marine Reserve and Rancho Marino sites. The average percent cover of *P. limitata* was similar in the mid and mid-high zones at each site, but the cover was much higher at Bodega Marine Reserve than at Rancho Marino Reserve (Figure 2.1B and 2.1C). The percent cover of *P.*

californica was similar in the mid and mid-high zones at Corona del Mar (Figure 2.1D). *P. californica* was present at the Rancho Marino and Corona del Mar sites. At Rancho Marino, where *P. californica* is rare and patchy, we only surveyed and established plots within the *P. limitata* zone.

Rockweed presence was generally associated with higher mobile invertebrate species richness and abundance across quadrats at all three sites. Mobile invertebrate richness was always higher where *Silvetia* was present in all three zones where this species of rockweed was found. With the exception of the mid-intertidal zone in the Bodega Marine Reserve, we observed a similar pattern for mobile invertebrate abundance in plots with and without *Silvetia*. At all sites, the presence of *Pelvetiopsis* was associated with higher mobile invertebrate richness and abundance in the highest zone where *Pelvetiopsis* was found.

The relationship between rockweeds and mobile invertebrate richness and abundance in the Bodega Marine Reserve depended on tide height (Richness: two-way ANOVA: tide height, $p = 0.06$; rockweed, $p = 0.05$; tide height x rockweed, $F = 16.72$, $p < 0.001$, Figure 2.2A; Abundance: two-way ANOVA: tide height, $p = 0.08$; rockweed, $p = 0.06$; tide height x rockweed, $F = 18.12$, $p < 0.001$; Figure 2.2B). The presence of *Silvetia* only increased mobile invertebrate species richness in the low zone ($p = 0.03$). *Pelvetiopsis* increased mobile species richness and abundance in the highest zone where *Pelvetiopsis* was present (Richness and Abundance: $p < 0.001$).

The relationship between rockweeds and mobile invertebrate richness and abundance at Rancho Marino depended on tide height (Richness: two-way ANOVA: tide height, $p = 0.08$; rockweed, $p = 0.04$; tide height x rockweed, $F = 11.22$, $p < 0.001$; Figure 2.2C; Abundance: two-way ANOVA: tide height, $p = 0.06$; rockweed, $p = 0.05$; tide height x rockweed, $F = 14.62$, $p =$

0.03; Figure 2.2D). Mobile species richness was significantly higher in low ($p < 0.001$) and mobile richness and abundance was higher in the low-mid plots (Richness: $p = 0.01$, Abundance: $p < 0.001$) where *Silvetia* was present and in mid-high plots when *Pelvetiopsis* was present (Richness: $p < 0.001$; Abundance: $p = 0.04$).

The relationship between rockweeds and mobile invertebrate richness at Corona del Mar depended on tide height (Richness: two-way ANOVA: tide height, $p = 0.03$; rockweed, $p = 0.03$; tide height x rockweed, $F = 13.45$, $p < 0.001$; Figure 2.2E; Abundance: two-way ANOVA: tide height, $p = 0.04$; rockweed, $p = 0.05$; tide height x rockweed, $F = 10.17$, $p < 0.001$; Figure 2.2F). Plots with rockweed species present had higher mobile invertebrate richness abundance than plots without rockweed; these differences were only significant for *Pelvetiopsis* in the highest zone (Richness: $p = 0.03$; Abundance: $p = 0.02$) and in the mid zone for *Silvetia* ($p = 0.01$).

At the mid-point of the tidal distribution of *Pelvetiopsis,* percent cover of seaweeds decreased from north to south (Figure 2.3). At our northern and central sites, cover of branched (*Endocladia*) and bladed species (*Mastocarpus*) was higher than unoccupied "bare" space, but at Corona del Mar bare rock and non-coralline crusts dominated the available space in the *Pelvetiopsis* zone. Similarly, at the mid-point of the distribution of *Silvetia*, seaweed cover was higher and bare space was lower at Bodega Marine Reserve and Rancho Marino than at Corona del Mar (Figure 2.4). At our northern and central sites, cover of branched (*Endocladia* and *Corallina*) and bladed species (*Mastocarpus* and *Mazzaella*) was higher than bare rock cover, but at Corona del Mar, bare rock and non-coralline crusts dominated the available space.

Removal experiment

The richness and abundance of mobile invertebrates were similar at Bodega Marine Reserve and Rancho Marino. The richness and abundance of mobile invertebrates was similar over time regardless of the presence or absence of *Pelvetiopsis* or *Silvetia* (Figures 2.5A-2.5D, 2.6A-2.6; See Supplementary Tables 1-4 and 7-10).

For *Pelvetiopsis* plots at Corona del Mar, the effect of treatment on the richness of mobile invertebrates changed over time (Repeated-measures ANOVA: Month x Treatment $p = 0.04$, See Supplementary Table 5, Figure 2.5E). Initially, removal plots were to similar control plots, but over time removal plots became more similar to "no rockweed" plots. For *Pelvetiopsis* plots, the effect of treatment on the abundance of mobile invertebrates changed over time (Repeated-measures ANOVA: Month x Treatment, $p < 0.05$; Supplementary Table 6, Figure 2.5F). After nine months, the removal plots and "no rockweed" plots were significantly different from the control plots (control vs. removal, $p = 0.01$; control vs. "no rockweed", $p = 0.02$), and this trend continued until the end of the experiment. Average mobile invertebrate richness and abundance were lowest at Corona del Mar compared to our other two sites.

For *Silvetia* plots at Corona del Mar, the effect of treatment on the richness of mobile invertebrates changed over time (Repeated-measures ANOVA: Month x Treatment, $p < 0.05$; Supplementary Table 11, Figure 2.6E). Initially, removal plots were similar to control plots, but over time removal plots became more similar to "no rockweed" plots. After nine months, the removal plots and "no rockweed" plots were significantly different from the control plots for mobile invertebrate richness (control vs. removal, $p = 0.01$; control vs. "no rockweed", $p = 0.01$) and this trend continued until the end of the experiment. For *Silvetia* plots, the effect of treatment on the abundance of mobile invertebrates changed over time (Repeated-measures ANOVA:

Month x Treatment, $p < 0.05$; See Supplementary Table 12, Figure 2.6F). After six months, the removal plots and "no rockweed" plots were significantly different from the control plots (control vs. removal $p = 0.02$; control vs. "no rockweed" $p = 0.03$) and this trend continued until the end of the experiment.

There was no difference in the community composition of plots in the *Pelvetiopsis* zone at the beginning and end of the experiment at Bodega Marine Reserve (PERMANOVA: $p = 0.74$) or at Rancho Marino (PERMANOVA: $p = 0.64$). At Corona del Mar, we observed significant differences between the initial and final mobile invertebrate communities when *Pelvetiopsis* was removed (PERMANOVA: $p < 0.001$). A SIMPER analysis indicated that the species that contributed the most to the difference between communities were the limpets *Lottia scabra* and *Lottia austradigitalis* and the snail *Littorina* sp. Twelve months after *Pelvetiopsis* was removed, these species had all declined in abundance.

Similarly, there was no difference in the community composition of plots in the *Silvetia* zone at the beginning and end of the experiment at Bodega Marine Reserve (PERMANOVA: $p = 0.61$) or at Rancho Marino (PERMANOVA: $p = 0.69$). When *Silvetia* was removed from plots at Corona del Mar there was a significant difference in mobile invertebrate communities (PERMANOVA: $p < 0.05$). The species that contributed the greatest differences between communities were the barnacle *Fissurella volcano,* the snail *Chlorostoma funebralis,* and the chiton *Cyanoplax hartwegii,* all of which declined in abundance over the 12-month experiment.

Discussion

We found that the role of rockweeds as foundation species changed along a latitudinal gradient. Rockweeds at our central and northern sites played a less important role in structuring

mobile invertebrate communities than rockweeds at our most southern site. At our southern site, removal of rockweeds appreciably decreased the richness and abundance of mobile invertebrate species in our plots (Figure 5E, 5F, 6E, and 6F). The differences in results between our observational study and removal experiment can be attributed to the location of plots. Removal plots were only in the central part of tidal distribution. Additionally, to find areas where rockweeds were naturally absent tended to be in areas that were inhospitable.

One potential factor underlying the latitudinal differences could be changes in air temperatures, which could alter the importance of these foundation species; average air and water temperatures increased by 7^{o}C from north to south. In particular, the warmer air temperatures at our southern site may make rockweeds more important for stress amelioration. Changes in the importance of rockweeds as facilitators have been documented along the New England coast, where *Ascophyllum* only facilitates associated species at more thermally stressful southern locations (Leonard 2000).

Additionally, rockweeds may be functionally redundant at our northern and central sites, where a number of alternative seaweed species co-occur that could provide stress amelioration (Figure 3A, 3B, 4A and 4B). Thomsen and South (2019) found that removal of the brown alga *Durvillaea* spp., also in the Fucales, allowed for alternative foundation species to colonize plots, altering the interactions among understory species. This is consistent with observations at Bodega Marine Reserve and Rancho Marino, where several species of bladed and branching seaweeds (e.g., *Mazzaella*, *Mastocarpus*, *Endocladia*, *Corallina*) co-occurred with our target rockweeds and seem to have compensated for their loss. However, at Corona del Mar there were few alternative seaweed species for mobile invertebrates to use as habitat when rockweeds were removed. Prior to establishing our treatments, a large proportion of plots at Corona del Mar

contained bare rock or non-coralline crusts, which would force the mobile invertebrates to move outside the plots to find suitable habitat when rockweeds were removed (Figure 3C and 4C). Lastly, we found that *Silvetia* and *Pelvetiopsis* play similar roles in their respective tidal zones at Corona del Mar. The pattern of decline following removal of these foundation species was similar in terms of both richness and abundance of mobile invertebrates. This indicates that in a thermally stressful environment these rockweeds are collectively and sequentially extending the range of many mobile invertebrates into higher tidal zones than would be possible if these rockweeds were not present.

Multiple other studies have investigated how the removal of fucoid species impacts grazer community dynamics (Speidel et al. 2001, Schiel and Lilley 2007, Crowe et al. 2013). Speidel et al. (2001) found that removal of *Fucus gardneri* in Washington did not change the mobile invertebrate community in their plots. Similarly, Schiel and Lilley (2007) removed *Hormosira banksii* from low intertidal plots in New Zealand and found no change in the mobile invertebrate community. Similar to these two studies, we found no change in the richness and abundance of mobile invertebrates at two of our three study sites. *F. gardneri* replaces *Silvetia* in the mid intertidal zone north of Humboldt County, California, therefore, the effect of these two rockweed species is consistent across a large geographic range when abiotic conditions are less thermally stressful.

As temperatures continue to increase as a result of climate change, biodiversity is under threat and is predicted to decline (IPBES 2016). An increase in temperatures can allow invasive species to colonize an area previously maintained by a native foundation species (Thomsen and South 2019). Rising temperatures are likely to alter trophic interactions. For example, Petchey et al. (1999) found that more diverse assemblages buffered communities against the effects of

warming, allowing the community to maintain its structure and functioning. We found a decline in mobile invertebrate diversity at our most southern site, which is likely to cause changes in grazing patterns. Changes in grazing could lead to changes in both the micro- and macroalgal communities (O'Connor et al. 2015). Rockweeds are declining, especially in southern California, making it critical to understand their role in structuring communities, especially in the context of predicting the impacts of climate change (Thom and Widdowson 1978, Gunnill 1980, Whitaker et al. 2010). Maintaining diversity is essential to help mitigate the effects of climate change and maintain ecosystem function.

A shift in community composition, such as the one associated with the loss of foundation species, can lead to changes in ecosystem functioning (Ellison 2019). The extinction of a foundation species can cause the coextinction of multiple other species that are associated with the foundation species, especially those with co-evolved relationships. Koh et al. (2004a) found that the relationship between host extinctions and affiliated species among a variety of taxa was nearly one to one. For example, Koh et al. (2004b) found that the snout moth had gone locally extinct in Singapore because of the extinction of the plant that supports its larval stage. The loss of *S. compressa* from southern California rocky shores could similarly lead to the coextinction of *Cyanoplax*, which is virtually always found in association with *Silvetia* (Sapper and Murray 2003). Koh et al. (2004a) estimate that based on the current list of endangered species there are 6,300 species that are also at risk of extinction because of their relationship with an endangered species. One of the major challenges with making generalizations about biodiversity loss in different systems is environmental heterogeneity and differences in the responses of species in different locations (Balvenera et al. 2006). Our study further demonstrates the importance of

studying the drivers of species loss at multiple locations because of the variability in the response of communities.

Table 2.1 Tidal distribution (m) of *Silvetia* and *Pelvetiopsis* at each site and average air and water temperature at each site. Temperatures were measured using TidBit temperature loggers placed within the rockweed zone.

	***Silvetia* tidal distribution (meters)**	***Pelvetiopsis* tidal distribution (meters)**	**Average (±SD) air temperature (^{o}C)**	**Average (±SD) water temperature (^{o}C)**
Bodega Marine Reserve	0.7-1.5	1.5-2.1	12.8 (±9.7)	10.1 (±2.7)
Rancho Marino	0.6-1.2	1.2-1.9	15.1 (±7.3)	13.6 (±2.1)
Corona del Mar	0.2-0.9	0.9-1.3	18.9 (±9.6)	17.4 (±3.7)

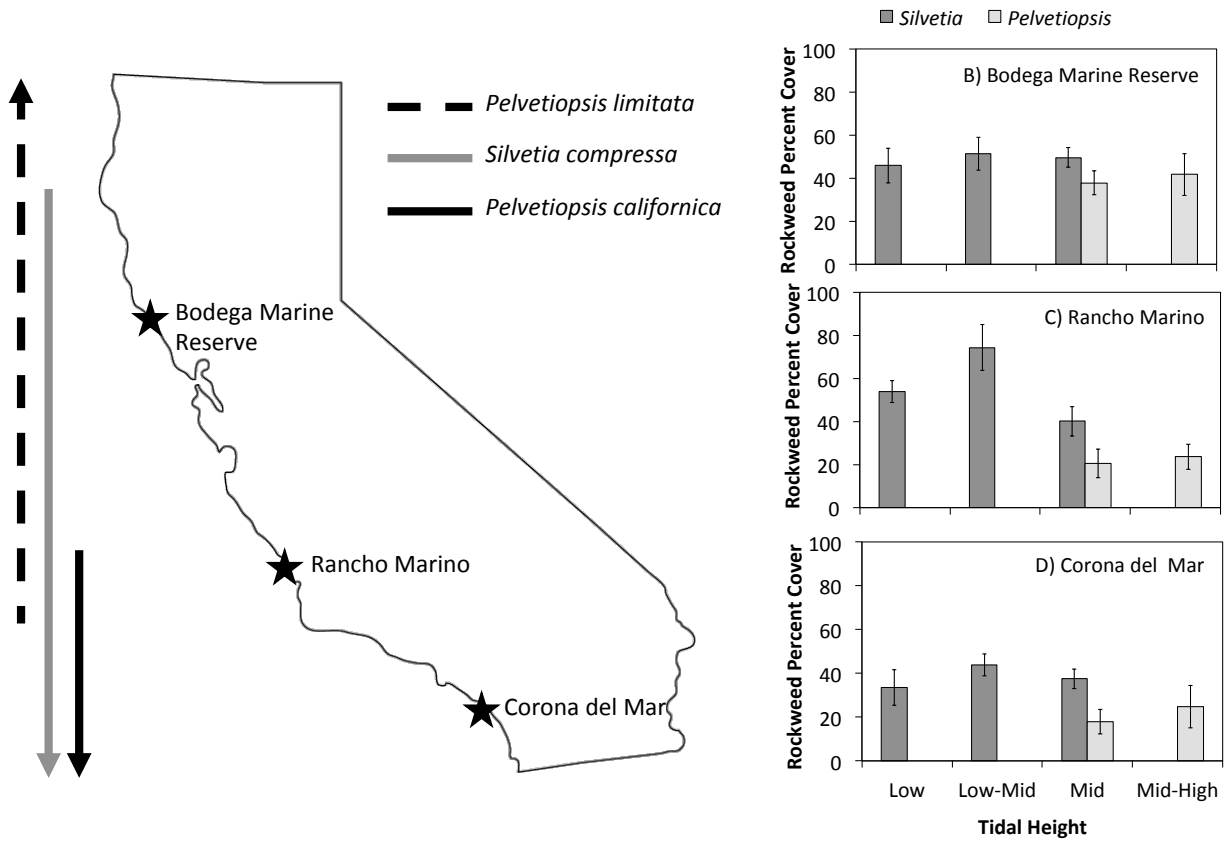

Figure 2.1 A) Location of study sites and the distribution within California of three rockweed species. Average rockweed percent cover (±SEM) by effective tide height in B) Bodega Marine Reserve C) Rancho Marino D) Corona del Mar

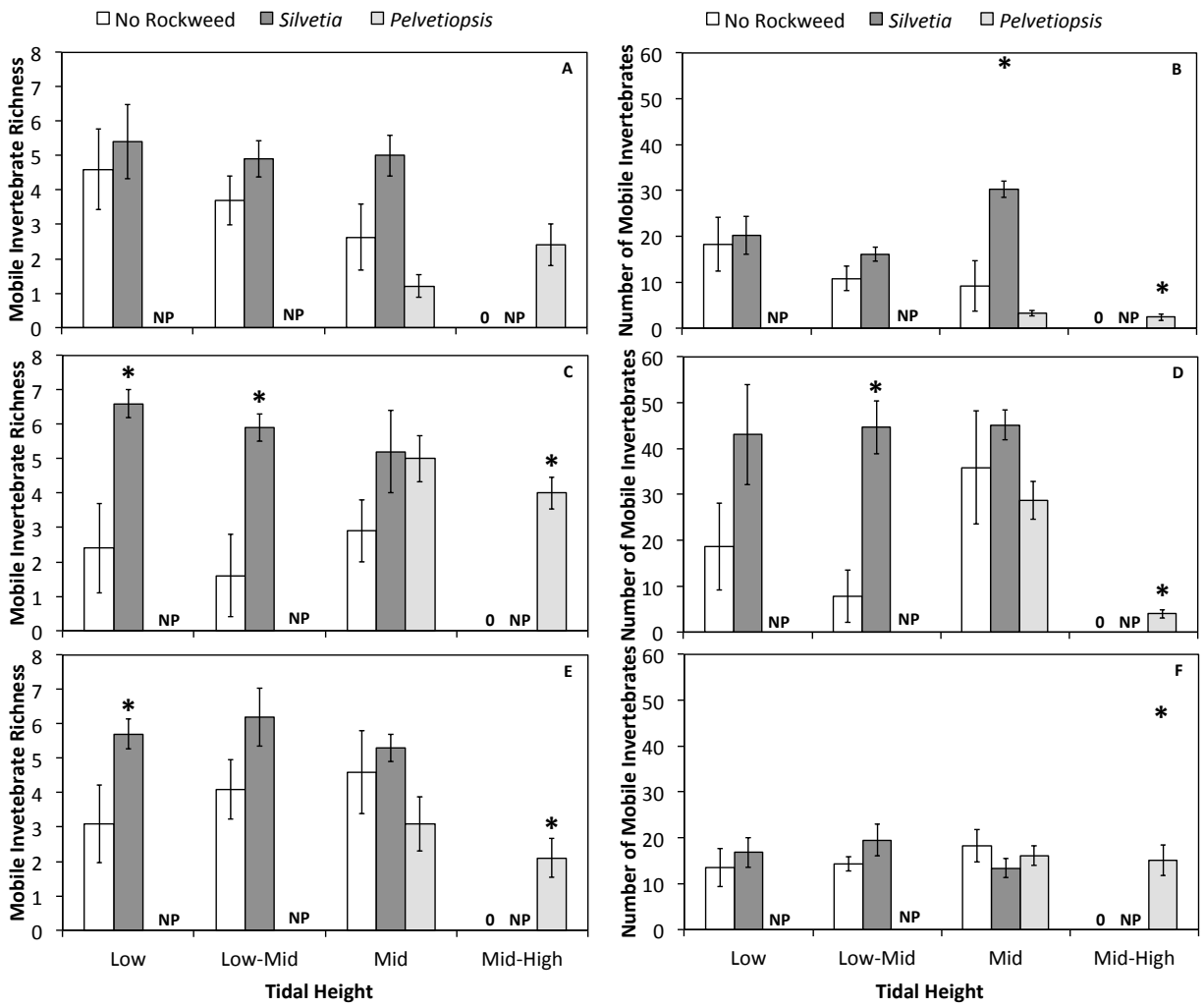

Figure 2.2 Average (±SEM) richness and abundance (individuals per 0.25 m^2) of mobile invertebrates in survey plots with and without *Silvetia* and *Pelvetiopsis*. A) Bodega Marine Reserve richness B) Bodega Marine Reserve abundance C) Rancho Marino richness D) Rancho Marino abundance E) Corona del Mar richness F) Corona del Mar abundance Note: NP indicates rockweed species not present, * indicates significant difference between plots ($p < 0.001$).

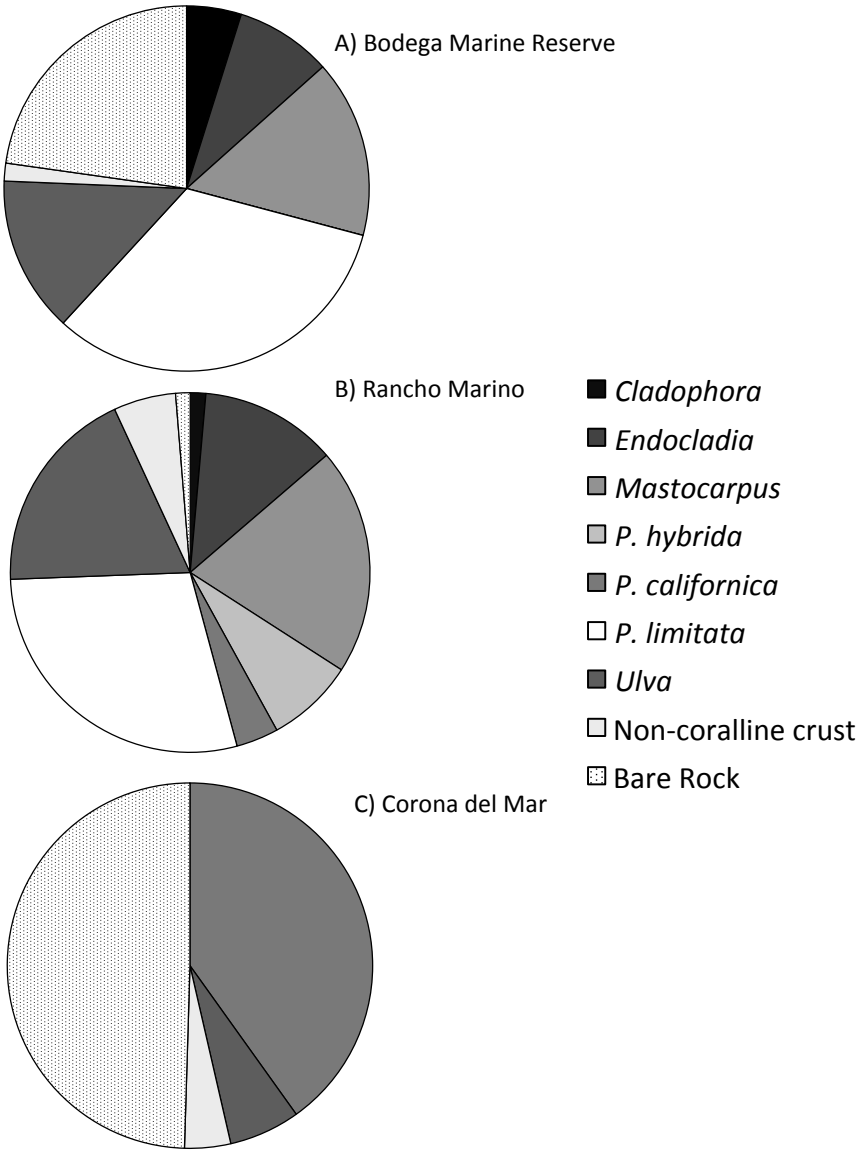

Figure 2.3 Percent cover of seaweeds in *Pelvetiopsis* zone plots prior to establishing experimental treatments at each site. A) Bodega Marine Reserve B) Rancho Marino C) Corona del Mar

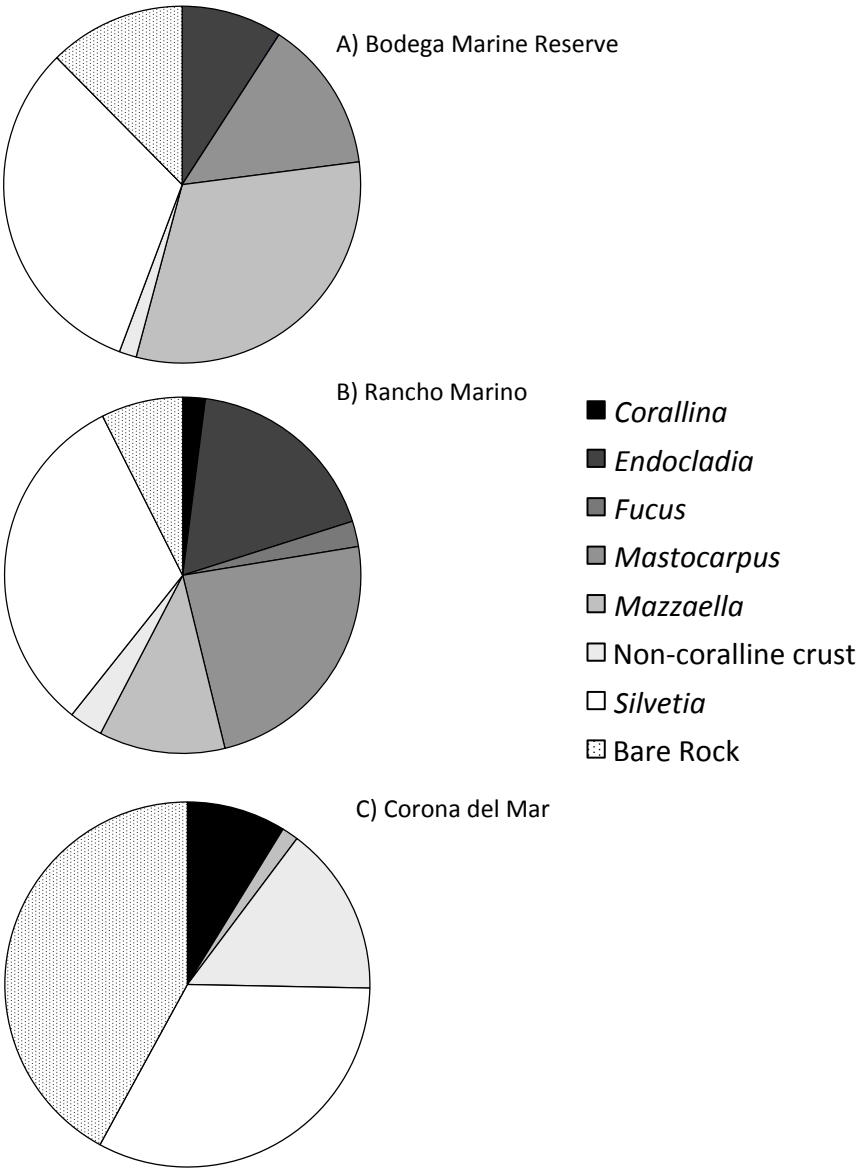

Figure 2.4 Percent cover of seaweeds in *Silvetia* zone plots prior to establishing experimental treatments at each site. A) Bodega Marine Reserve B) Rancho Marino C) Corona del Mar

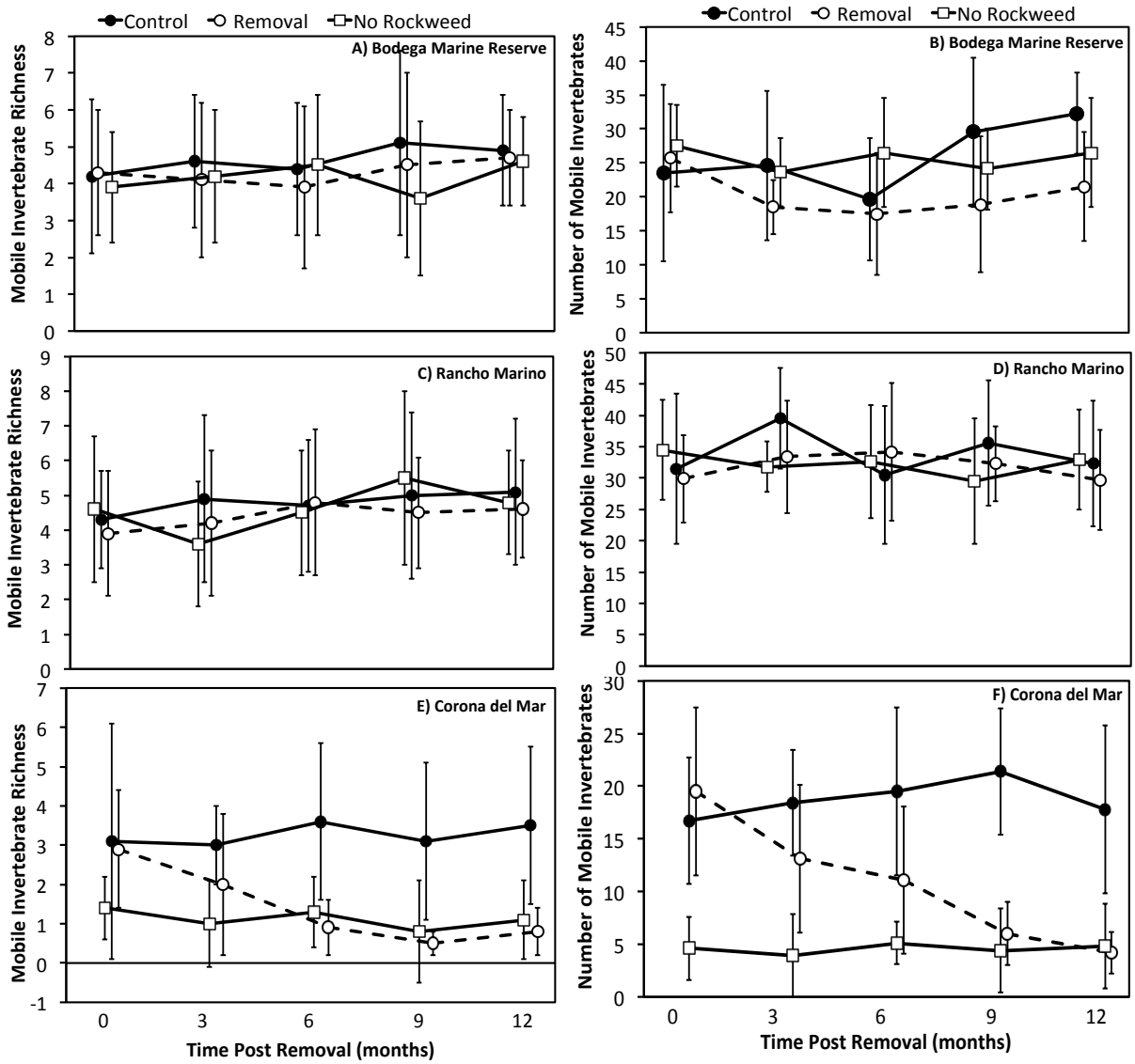

Figure 2.5 Average (±SEM) richness and abundance (individuals per 0.25 m^2) of mobile invertebrates in control and removal plots of *Pelvetiopsis*. A) Bodega Marine Reserve Richness B) Bodega Marine Reserve abundance C) Rancho Marino richness D) Rancho Marino abundance E) Corona del Mar richness F) Corona del Mar abundance Note: Points are offset to allow better visualization.

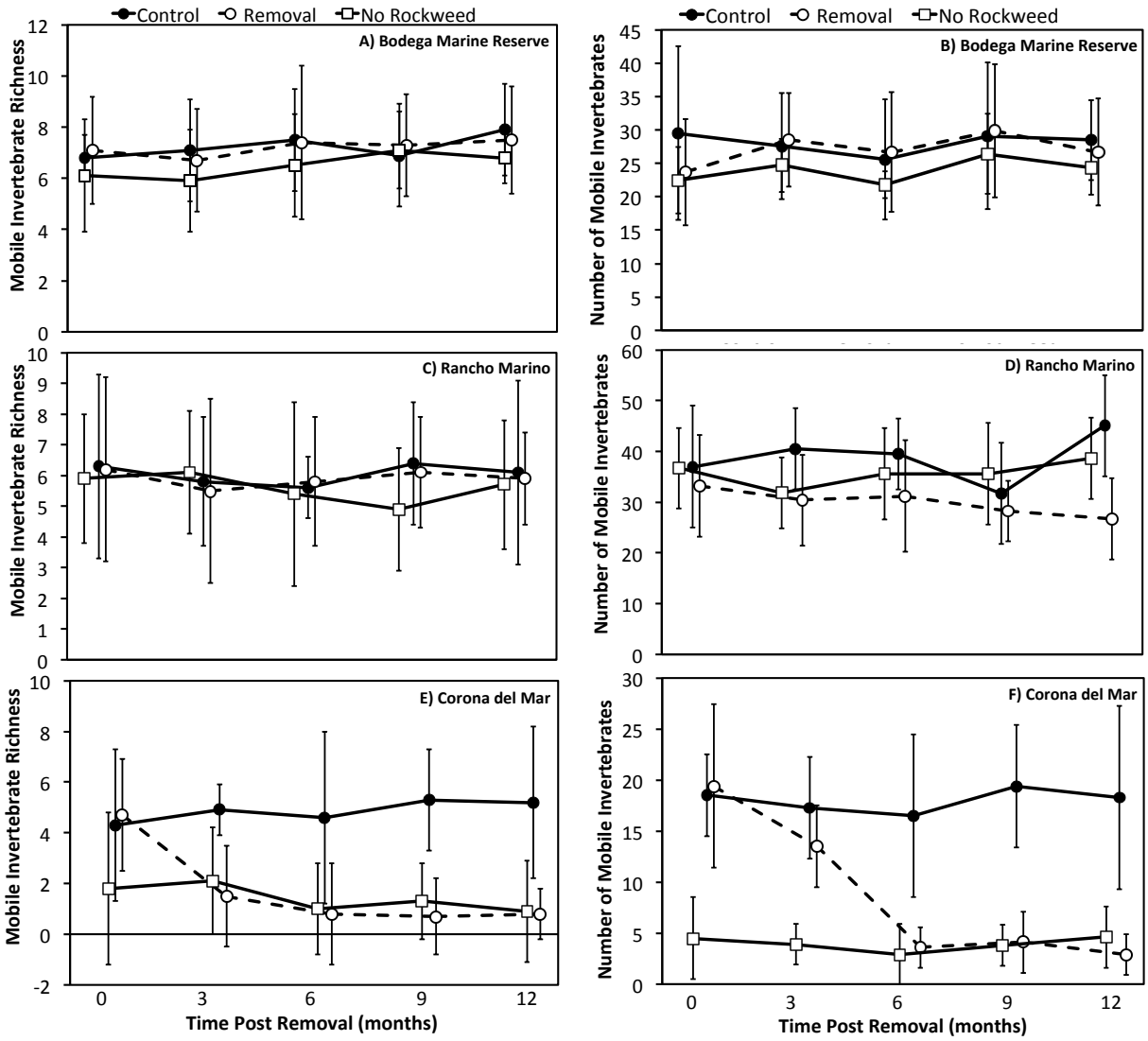

Figure 2.6 Average (±SEM) richness and abundance (individuals per 0.25 m^2) of mobile invertebrates in control and removal plots of *Silvetia*. A) Bodega Marine Reserve richness B) Bodega Marine Reserve abundance C) Rancho Marino richness D) Rancho Marino abundance E) Corona del Mar richness F) Corona del Mar abundance Note: Points are offset to allow better visualization.

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CHAPTER 3

Population demographic characteristics of two foundation species in the centers and at the edges of their biogeographic ranges

Abstract

Understanding the factors determining species' geographic range limits is important for making predictions about how the distributions of organisms will change over time. The Abundant Center Hypothesis states that range-edge populations should have lower growth, reproduction, and survival than range-central populations, leading to reduced abundances. Studying edge populations vs. central populations is important for making informed conservation decisions to preserve species variation in the face of climate change. We studied demographic characteristics of two foundation species, the intertidal seaweeds *Silvetia compressa* and *Pelvetiopsis limitata*, at four locations within each species' geographic range. We studied the populations at two sites at the leading (poleward) edge and two sites in the central part of the geographic range of *Silvetia*. For *Pelvetiopsis*, we studied two populations at the trailing (equatorward) edge and two populations in the central part of the geographic range. For a 12-month period, we measured the size, survival, and reproductive output of 100 individuals across sizes of each species to construct integral projection models for each species at each site. We found that for *Silvetia*, northern-edge and range-central populations had similar vital rates, refuting the Abundant Centre Hypothesis. In contrast, we found that southern edge populations of *Pelvetiopsis* had lower population growth rates, were smaller in size, had lower survival, and had lower reproductive output than populations at the center of the range. Our results indicate that spatial variation in demographic rates – particularly between edge and central populations – differs between rockweed species and/or the edge (trailing or leading) under investigation. Since rockweeds play an important role in maintaining overall community diversity, recently observed declines of southern-edge populations may be a precursor to overall reduction in biodiversity and ecosystem functioning along California rocky shores.

Introduction

Along species' biogeographic ranges, leading edge, trailing edge, and central populations each experience different abiotic environments, which can lead to differences in morphology and reproductive characteristics (Lesica and Allendorf 1995). The environmental gradients often associated with geogrpahic ranges are important in determining the abundance and performance of a species throughout its range (Aikens and Roach 2014). It has been hypothesized that individuals in central populations are larger and more abundant than populations at the edge of the species' geographic distribution [i.e., the Abundant Center Hypothesis (ACH); Sagarin and Gaines 2002]. This hypothesis is based on the expectation that species' ranges are set by abiotic factors, and populations living close to range edges are likely to experience greater and more frequent abiotic abiotic stressors than central populations (Sorte and Hofmann 2004). Sagarin and Gaines (2002) tested the ACH by exmining data on changes in abundances across the biogeographic ranges of twelve coastal marine species, and they found that less than half of species actually provided support for this hypothesis. Many of species had abundances that either increased or decreased with latitude (Sagarin and Gaines 2002). This illustrates that the leading and trailing edges of a population may differ in their abundance and preformance. Understanding how populations function at different locations within a species' range can help researchers and managers make predictions about how species may respond to climate change. Additionally, this information can help determine whether or not species will be able to persist under future conditions.

Identifying vulnerable life history stages, size classes, and locations within a species' range is important for conservation and management efforts. One method for identifying these

stages is through demographic models that determine critical transitions across an organism's life history. The ability of individuals to survive to the next size category or transition to the next life history stage can be strongly impacted by the local environment. Not all life history stages may be equally important to the persistence of a species (Pandori and Sorte 2019). The response of individuals to abioitc stresses may vary extensively throughout a species' life history because of changing characteristics and strategies of each stage (Hamdoun and Epel 2007, Kapsenberg and Hofmann 2014). For example, larger individuals may be more tolerant to changes in environmental conditions than early stages because of acquired tolerance, which in turn can allow these individuals to transition to the next size category, or life history stage (Vetter 1999). Demographic models can help researchers identify the most vulnerable stage within an organisms' life history. Furthermore, demographic data can be used to determine which demographic attribute is most strongly affected by changes in the environment.

Rocky intertidal rockweed species are ideal organisms for studying how the demographic characteristics of populations change based on location because adults are not mobile and rockweeds are characterized by relatively closed populations. The sessile nature of rockweeds makes it easier to follow specific individuals over time, allowing for determination of surivval and growth rates of specific individuals. During reproduction, a packet of zygotes settles near the adult individuals, so the typical disperal range of rockweeds is limited to a few meters or less (Johnson and Brawley 1998). A small diseprsal range can allow for a more effective estimation of reproduction per individual than would be possible for a species with mobile reproductive stages. These chracteristics can allow for accurate measurement of survival, growth and reproduction of rockweeds so that a demographic model can be created.

Rockweeds are foundation species, making their presence essential for maintaining ecosystem diversity and functioning (see Chapter 2). Rockweeds are declining along the California coast, and understanding their demographic characteristics is also important for informing that management efforts (MARINe 2018). Additionally, Peterson et al. (2003) found that the recovery of rockweeds following a disturbance can be extremely slow, taking years to reach pre-disturbance population levels. Lastly, there are multiple species of rockweeds found along the California coast (Abbott and Hollenberg 1992), which allows researchers to compare how closely related species differ in their demographic characteristics at a single location where two species' geographic range overlap.

We constructed integral projection models for two species of rockweeds at four different sites within the species' geographic ranges to examine the demographic chracteristics of trailing edge, leading edge, and central populations. We studied leading edge and central populations of *Silvetia compressa* and trailing edge and central populations of *Pelvetiopsis limitata.* We specifically addressed the following question: How do central and edge populations differ in growth, survival, and reproductive output? We hypothesized that edge populations would have reduced growth, reproduction, and survival compared to central populations.

Methods

Study Sites and Species

We monitored two species of rockweed - *Silvetia compressa* (J. Agardh) E.Serrão, T. O. Cho, S. M. Boo and Brawley and *Pelvetiopsis limitata* (Setchell) N. L. Gardner – at four sites from April 2018 to April 2019 (Figure 3.1). Sites included Point Arena-Stornetta Ranch Public Lands (38.9364° N, 123.7232° W), the University of California Bodega Marine Reserve (38.32°

N, 123.07° W), the University of California Kenneth S. Norris Rancho Marino Natural Reserve (35.56° N, 121.08° W), and Hazards Canyon Reef (35.2900° N, 120.8838° W).

The geographic distribution of *Silvetia compressa* is from Humboldt County, California, USA to Punta Baja, Baja California, Mexico (Silva 1990). Our sites at Bodega Marine Reserve and Point Arena are near the northern geographic range limit of *Silvetia*, while Rancho Marino and Hazards are in the central part of the species' geographic range. The geographic distribution of *Pelvetiopsis limitata* is from Vancouver Island, British Columbia, Canada to San Luis Obispo County, California, USA (Abbott and Hollenberg 1976). Rancho Marino and Hazards are near the southern range limit of *Pelvetiopsis*, and Bodega Marine Reserve and Point Arena are in the central part of its geographic range.

Data Collection

We used marine epoxy (Z-Spar A788 Splash Zone Compound, Kop-Coat Marine Group, Rockaway, New Jersey, USA) and combinations of colored zip ties to mark 100 individuals per species per site during April of 2018. Individuals were located in the upper and lower edges of each rockweed zone at each site, which was between 0.6 and 1.5 meters above mean lower-low water for *Silvetia* and between 1.5 and 2.0 meters above mean lower-low water for *Pelvetiopsis*. We randomly selected 20 individuals along a five-meter transect using a random number generator at each edge of the tidal distribution. An additional 30 individuals along each edge were haphazardly selected based on size so that a wide range of size classes were included. Each individual was counted monthly to assess survival and measured for length and circumference following the methods established by Åberg (1990). Monthly measurements were done based on previous work done by Skene (2009) at Bodega Marine Reserve. We estimated biomass (B) of each individual using the equation

$$B = L*c^2 \quad (1)$$

where L is the length of the individual and c is its circumference. We determined the relationship between the biomass estimate and dry mass by collecting 40 individuals spanning a range of sizes from each site and drying them to a constant mass at 60°C. We then used linear regressions to determine the relationship between biomass and dry weight (*Silvetia* $R^2 = 0.94$; *Pelvetiopsis* $R^2 = 0.93$). The dry weight of each individual was back calculated using the biomass estimates and regression equations. We also counted the number of branches with receptacles on each individual and counted the number of recruits within a 25 cm diameter circle around the individuals.

To estimate fecundity, we collected branches with receptacles from 20 untagged individuals at each site once per month from April to September 2018. Branches were collected from individuals of multiple size classes to provide reproductive estimates from individuals that represented the size distributions observed in the field. Untagged individuals were collected to avoid disturbing the tagged individuals that were being used to assess survival and growth. Branches were brought back to the lab and spawned following the methods established by Hays (2007) and Skene (2009). The number of eggs produced per receptacle for each species was counted, and fertilized zygotes were then pipetted onto travertine tiles. The number of attached zygotes was counted after 24 hours, and the tiles were then deployed in the field for two weeks. Tiles were placed under the canopy or within a group of the same rockweed species as the zygotes. After two weeks of field deployment, we counted the number of surviving zygotes on each tile. These measurements allowed us to estimate the number of offspring produced by the tagged individuals using the equation

$$O = (R \text{ x } E) \text{ x } \%S \quad (2)$$

where O is the number of offspring, R is the number of receptacles, E is the average number of eggs produced per receptacle, and $\%S$ is the percent survival of the zygotes.

Integral Projection Model Construction

To create our integral projection models (IPMs), we used procedures developed by Easterling et al. (2000). We used individual size as the state variable: the estimated dry weight of each individual at each census date. Linear regressions were used to establish relationships between size at time t and size at time $t + 1$, survival of individuals and size, and the number of offspring produced and size. Integrations were estimated using 100 discretized cells and the upper and lower limits were set based on the minimum size multiplied by 0.9 and the maximum size multiplied by 1.1. Demographic transitions (survival, growth and fecundity) were defined by the kernel function, $K(z'|z,x)$, where z' denotes the size at time $t + 1$ and z denotes the size at time t. The size distribution of individuals in the population from time t, given by $n(z, t)$, to time $t + 1$, given by $n(z', t + 1)$, is calculated by using the following integral

$$n(z', t+1) = \int_{\Omega} K(z'|z,x)n(z,t)dz \quad (3)$$

where Ω is the set of all possible sizes. The kernel can be further broken down into the growth/survival kernel, $P(z'|z)$ and the fecundity kernel, $F(z'|z)$ as

$$K(z'|z,x) = P(z'|z,x) + F(z'|z,x) \quad (4)$$

The growth/survival and fecundity kernels can be further broken down into functions specific to the life history of rockweeds and which can be estimated from regression. The growth/survival kernel can be expressed as

$$P(z|z,x) = s(z)\, g(z|z,x) \quad (5)$$

where $s(z)$ is the probability of survival as a function of individual size and $g(z|z,x)$ is the probability of growing from size z to size z' during one time step. The fecundity kernel is defined

by

$$F(z|z,x) = p(z)\, f(z,x) \quad (6)$$

where $p(z)$ is the probability of reproducing, and $f(z,x)$ is the number of zygotes that are produced by an individual at size z and survive. The fecundity estimate for each individual was calculated using the number of receptacles at each census date converted to the number of offspring using Eq. 2.

Using the IPM, we calculated the dominant eigenvalue λ that represents the population's growth rate. We also calculated the dominant right and left eigenvectors, *w(x)* and *v (x)*, which give the stable size distribution and size specific reproductive values. Sensitivity and elasticity values were calculated to determine the effect of changes of to fecundity and survival on population growth rate. All analyses were done using R with the stats and utils packages (R Core Team, 2015).

Results

Population Growth

The populations of *Silvetia* at all four sites were characterized by $\lambda < 1.0$ (Table 3.1). Values of λ were slightly higher at the range central sites (Hazards, $\lambda = 0.95$; Rancho Marino, $\lambda = 0.96$) than at the northern edge of the species range (Bodega Marine Reserve, $\lambda = 0.92$; Point Arena, $\lambda = 0.94$). Similar to *Silvetia,* λ values for *Pelvetiopsis* were less than 1.0 at all sites (Table 3.1). Population growth values were higher at range-central sites (Bodega Marine Reserve, $\lambda = 0.91$; Point Arena, $\lambda = 0.90$) than at southern edge sites (Hazards, $\lambda = 0.86$; Rancho Marino, $\lambda = 0.82$). Overall, population growth rates were higher for *Silvetia* than *Pelvetiopsis* across all sites.

Stable Size Distribution and Reproductive Value

At all sites the stable size distribution was skewed towards *Silvetia* and *Pelvetiopsis* with smaller sizes (Figure 3.2 and Figure 3.3). The stable size distributions were inconsistent with the observed size histogram-distribution of the data used to populate the model. At all sites for both species, populations could include individuals larger than the stable size distribution.

For *Silvetia*, the reproductive values of individuals at Hazards and Bodega Marine Reserve were highest at intermediate sizes. At Rancho Marino and Point Arena the reproductive value increased with increasing *Silvetia* dry weight (Figure 3.4). Reproductive value of *Pelvetiopsis* decreased with increasing size dry weight at all sites except Rancho Marino (Figure 3.5). At Rancho Marino, the reproductive value of *Pelvetiopsis* individuals increased with increasing size.

Sensitivity and Elasticity

Sensitivity values decreased with increasing size of individuals for both species and all sites (Figure 3.6 and Figure 3.7). Elasticity values were highest for the smallest individuals, especially for *Silvetia* at Bodega Marine Reserve (Figure 3.7c)

Discussion

We found that the populations of *Silvetia* and *Pelvetiopsis* are declining based on the population growth rates predicted from the model. However, the difference between range central and edge populations differed depending on whether the range edge studied was the

leading or trailing edge. The population growth rates of the leading edge and range-central populations of *Silvetia* were all similar indicating that the leading edge and range-central populations have similar demographic characteristics. In contrast, the trailing edge and range-central populations of *Pelvetiopsis* differed from one another, with trailing edge populations experiencing a much greater decline than range-central populations. This difference in population growth rate is likely a result of decreased survival and recruitment at the more thermally stressful range edge.

The stable size distributions of populations were similar to the dataset used to populate the model, with a skew towards smaller sized individuals (Figure 3.2 and 3.3). However, there were individuals that were measured with a higher biomass than the stable size distribution. The biomasses of two of the range-central and one of the leading edge populations were comparable, showing that the leading edge and range-central populations are similar to one another in terms of the distribution of individual sizes. In contrast, the biomass of trailing edge populations and range-central populations differed indicating that range-central populations are larger than trailing edge populations.

Elasticity analyses for both species in both regions indicate the importance of transitioning to a size where reproduction can occur and reproducing as early as possible. Sensitivity analyses for range-central and leading edge populations were similar, indicating the importance of survival and transition from the smallest size classes to the next size. The sensitivity analyses of the range-central and trailing edge populations indicated that it was more important for trailing edge populations to survive and transition to the intermediate size classes, while this was less important for range-central populations.

The two species of rockweeds used in our study can act as foundation species; these roles are particularly important in areas where environmental conditions are unfavorable and functional redundancy is low (see Chapter 2). Loss of a foundation species can cause major alterations in community composition and ecosystem functioning (Ellison et al. 2005). Multiple studies of *Silvetia*, *Pelvetiopsis*, and similar species have documented the importance of this group as a foundation species (Speidel et al. 2001, Schiel and Lilley 2007, Crowe et al. 2013 Best et al. 2014; Chapter 2). More specifically, Sapper and Murray (2003) have found a strong facilitative relationship between *Silvetia* and the chiton, *Cynaoplax hartwegii*. *Silvetia* and *Pelvetiopsis* have been documented to be declining in abundance (Gunnill, 1980, Whitacker et al. 2010, MARINe, 2018). Given the importance of these species, these declines have the potential to result in large changes in community competition and ecosystem functioning. Declining populations can be identified using integral projection models, allowing for targeted management of populations.

The demographic characteristics of leading edge populations may be more similar to range-central populations. Villellas et al. (2013) studied populations of the annual plant *Plantago coronopus* at the leading edge and in the central part of its geographic range in Norway. Similar to our results, Villellas et al. (2013) did not find differences in the vital rates of the populations at the two locations they studied within the species' geographic range. Similarly, Wagner et al. (2011) found little difference in the vital rates of the steppe grass, *Stipa capillata*, across a 3000 km range in Eurasia. It is possible that leading edge populations are more likely to exhibit similar vital rates to central populations because of the similarity of environmental conditions. However, the ability of these leading edge populations to persist and expand under the current predictions

for climate change may be hindered by competition with established species (Scheller and Mladenoff 2008).

The characteristics that we found for *Pelvetiopsis* populations are consistent with other demographic studies on seaweeds. Viejo et al. (2011) studied populations of *Fucus serratus* along its geographic range in Europe. They found that trailing edge populations had fewer reproductive individuals and a higher number of small individuals compared to range central populations, which has led to a decline in populations at the range margin (Viejo et al. 2011). A similar study by Assis et al. (2013) on the kelp, *Laminaria hyborea* made predictions about the future of kelp populations throughout its geographic range and found that trailing edge populations are more likely to decline because of the harsh abiotic conditions associated with the southern margin of the range. In contrast to these two studies, Araújo et al. (2015) found that growth rates were similar at both range central and trailing edge populations of *Ascophyllum nodosum*, but that trailing edge populations in Europe had a higher reproductive investment. Based on these studies and our results, there does not appear to be a consistent pattern as to whether southern edge populations of seaweeds are under threat of extinction.

When making predictions about drivers of species geographic limits it is important to take into account different factors affecting species at different range edges. For example, our hypothesis was supported for an equatorward range edge that appears to be set by physiological stress. However, it was not supported for a poleward range edge that appears to be set by competitive interactions or dispersal limitation. Responses of equatorward-edge populations to small-scale changes in environmental factors are important for making accurate predictions of range contractions in response to climate change (Sagarin et al. 2006, Westerbom et al. 2019). For example, abundances in range-edge populations of the mussel *Mytilus trossulus* are driven

primarily by small changes in salinity and other environmental variables because these populations are already at their physiological limits (Westerbom et al. 2019). Chang et al. (2018) found similar patterns when observing sessile estuarine communities, where the composition of sessile invertebrate communities completely changed following a shift in environmental conditions. Environmental changes may also lead to local extinction events that create a patchy distribution at the trailing edge of a species' distribution (Sheth and Angert 2017, Vilà-Cabrera and Jump 2019).

At the leading edge of a species geographic range, competition and dispersal can be important factors to consider when making predictions about the populations dynamics of a species (Scheller and Mladenoff 2008). Elton's diversity invasion hypothesis states that diversity can be used to estimate the level of inter-specific competition among species (Elton 1958). For example, Meirer et al. (2012) found that in high-diversity areas, the establishment of tree saplings was lower compared to sites where few species are present. For the sites included in this study, my previous research found that the diversity of widespread species is higher at our more northern locations than at locations near a biogeographic boundary (Elsberry et al. 2018). Species with local dispersal are less likely to escape local competitors via dispersal (Scheller and Mladenoff 2008). The biogeographic ranges of trees with short dispersal distances rarely shift via dispersal (Scheller and Mladenoff 2008). Similar to trees, rockweeds tend to have short dispersal distances, making it difficult for leading edge populations to migrate in response to environmental changes (Johnson and Brawley 1999). These dynamic processes can make it difficult to make predictions about the resiliency of northern edge populations (Meirer et al. 2012).

Based on our results and those of other studies that have examined peripheral vs. range-central populations of a variety of organisms, locations occupied by peripheral populations are important for management and conservation (Lesica and Allendorf 1995). For example, Nakabayashi et al. (2019) found that range-edge populations of corals had lower genetic diversity, making these populations important targets for conservation because they lack the genetic variation to adapt to changing conditions. Additionally, these populations may have become locally adapted to stressful conditions. Leading-edge populations may be important for conservation efforts because some species may expand their ranges poleward as their equatorward range contracts. It is important to study and understand the population demographics of populations spanning the geographic range of a species in order to make effective conservation and management decisions (Suchan et al. 2019).

Table 3.1 Population growth rate of *Silvetia* and *Pelvetiopsis* at each site based on the eigenvalues of each model

Species	Location within Distribution	Site	λ
Silvetia	Central	Hazards	0.95
Silvetia	Central	Rancho Marino	0.96
Silvetia	Leading Edge	Bodega Marine Reserve	0.92
Silvetia	Leading Edge	Point Arena	0.94
Pelvetiopsis	Trailing Edge	Hazards	0.86
Pelvetiopsis	Trailing Edge	Rancho Marino	0.82
Pelvetiopsis	Central	Bodega Marine Reserve	0.91
Pelvetiopsis	Central	Point Arena	0.90

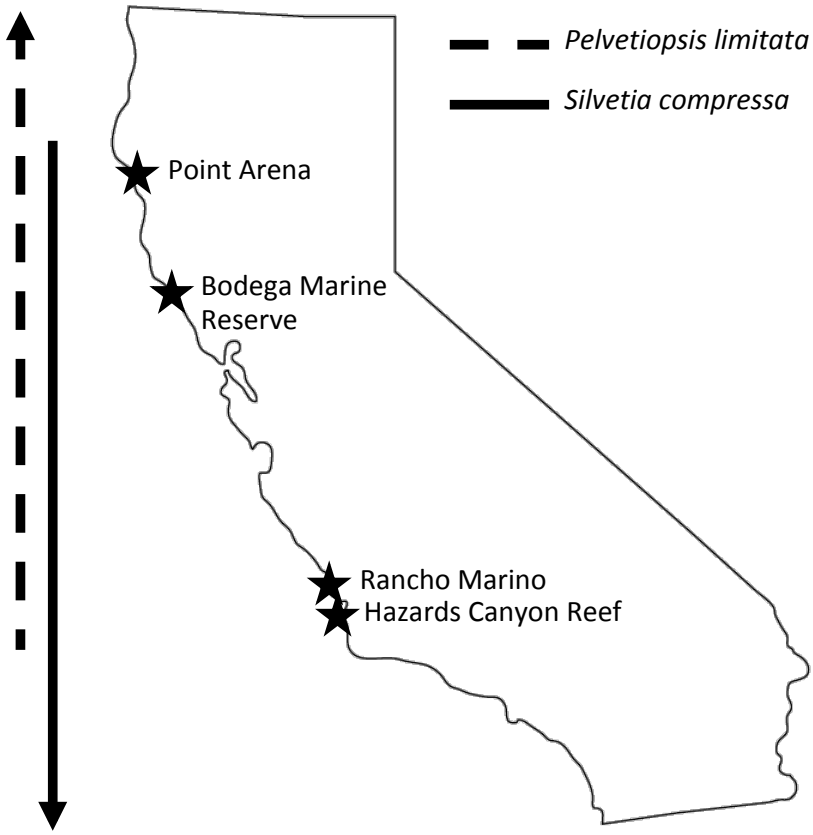

Figure 3.1 Location of study sites and the distribution of *Silvetia compressa* and *Pelvetiopsis limitata* within California, USA.

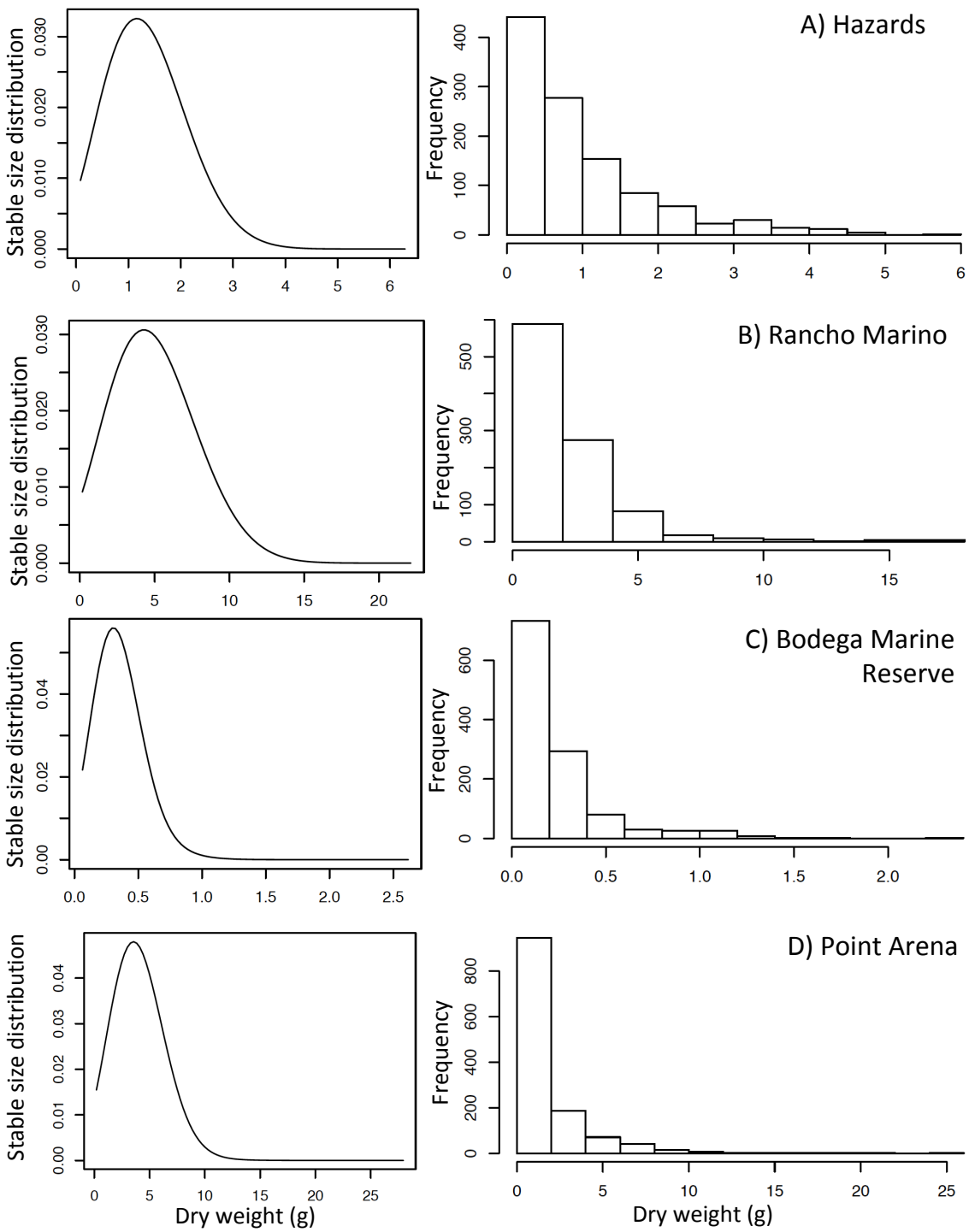

Figure 3.2 Stable size distribution for the integral projection of *Silvetia* at each site and histogram distribution of dry weights (g) of individuals. The x- and y-axis scales are different among the panels.

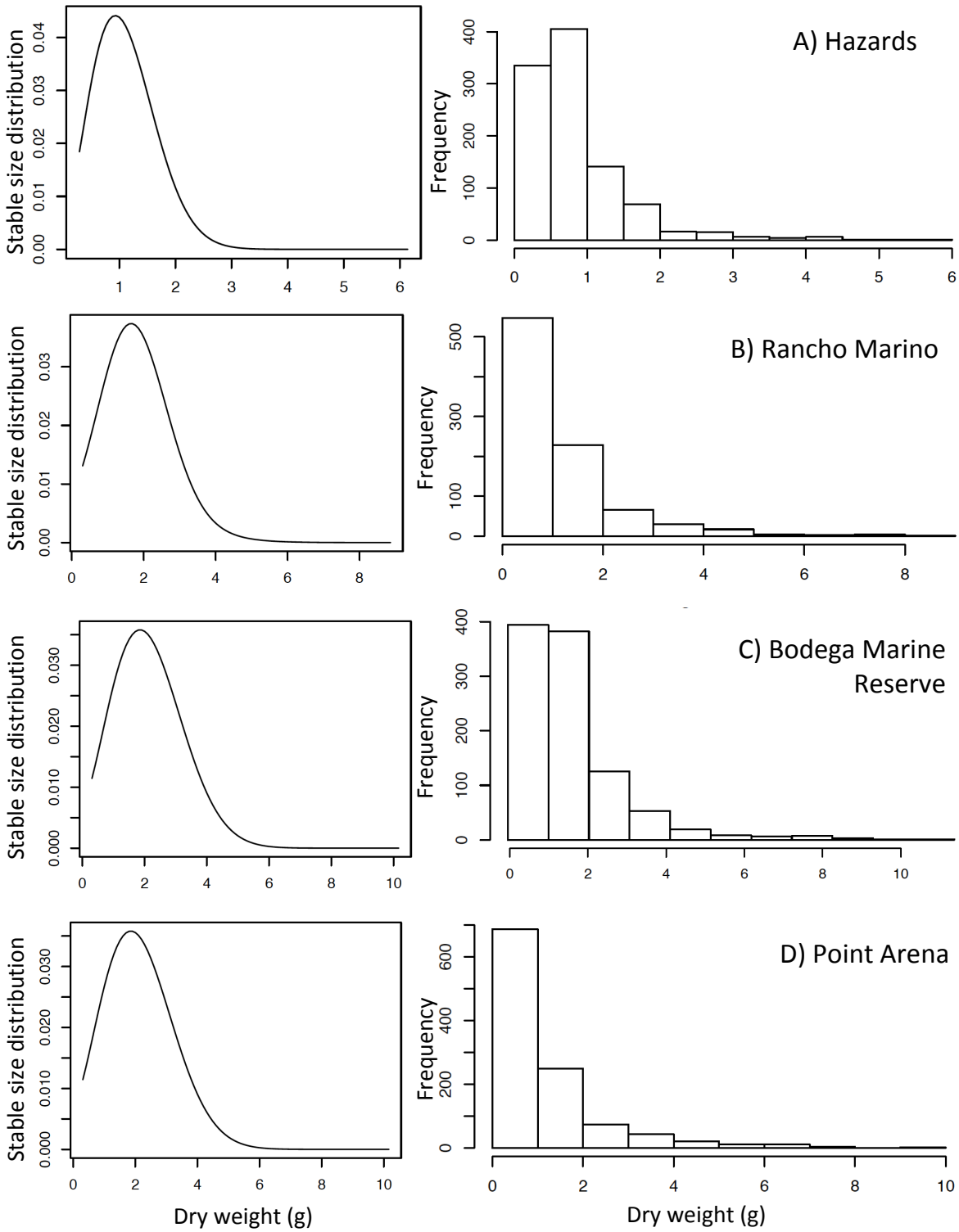

Figure 3.3 Stable size distribution for the integral projection of *Pelvetiopsis* at each site and histogram distribution of dry weights (g) of individuals. The x- and y-axis scales are different among the panels.

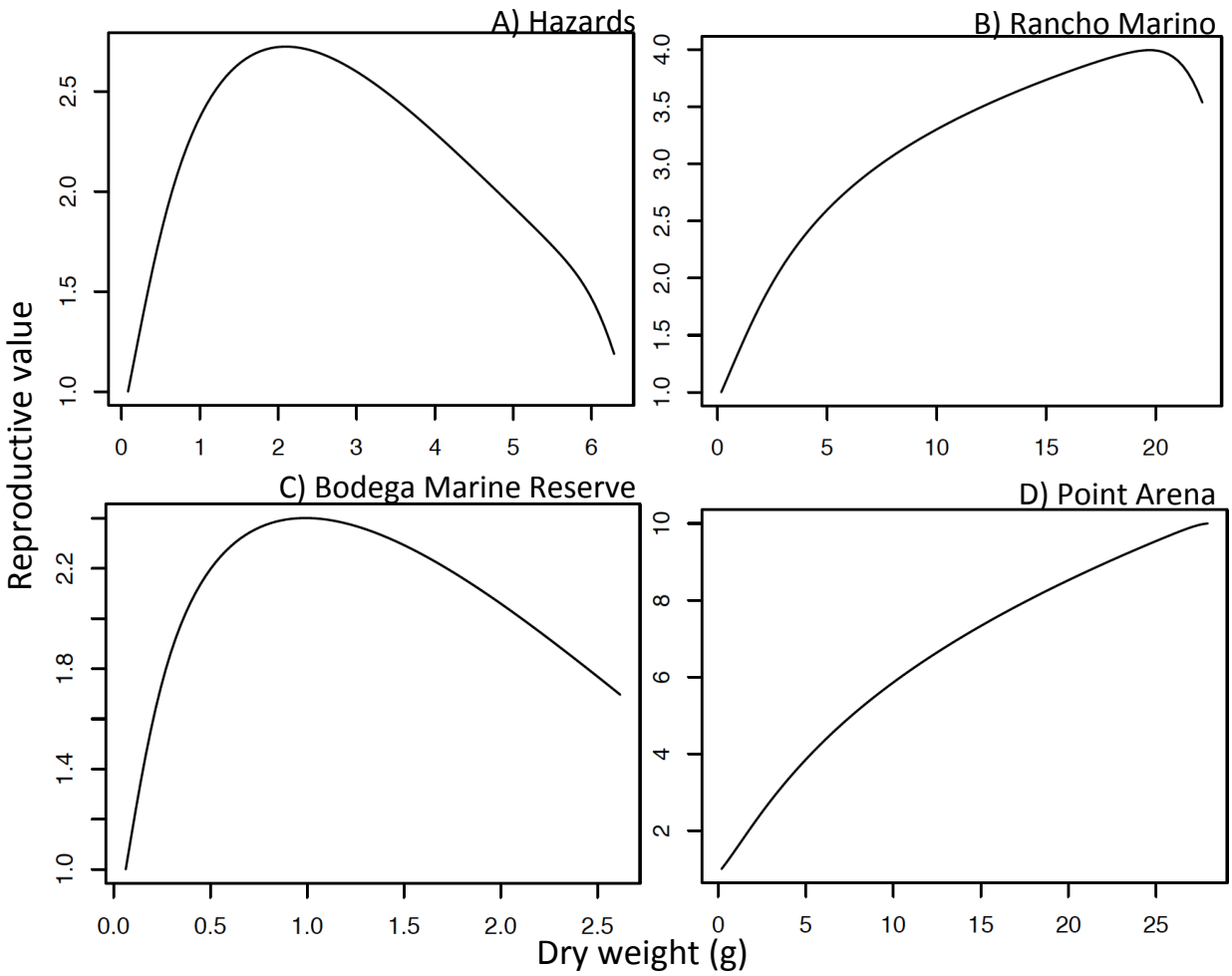

Figure 3.4 Relative reproductive value for the integral projection model of *Silvetia* at each site. The x- and y-axis scales are different among the panels.

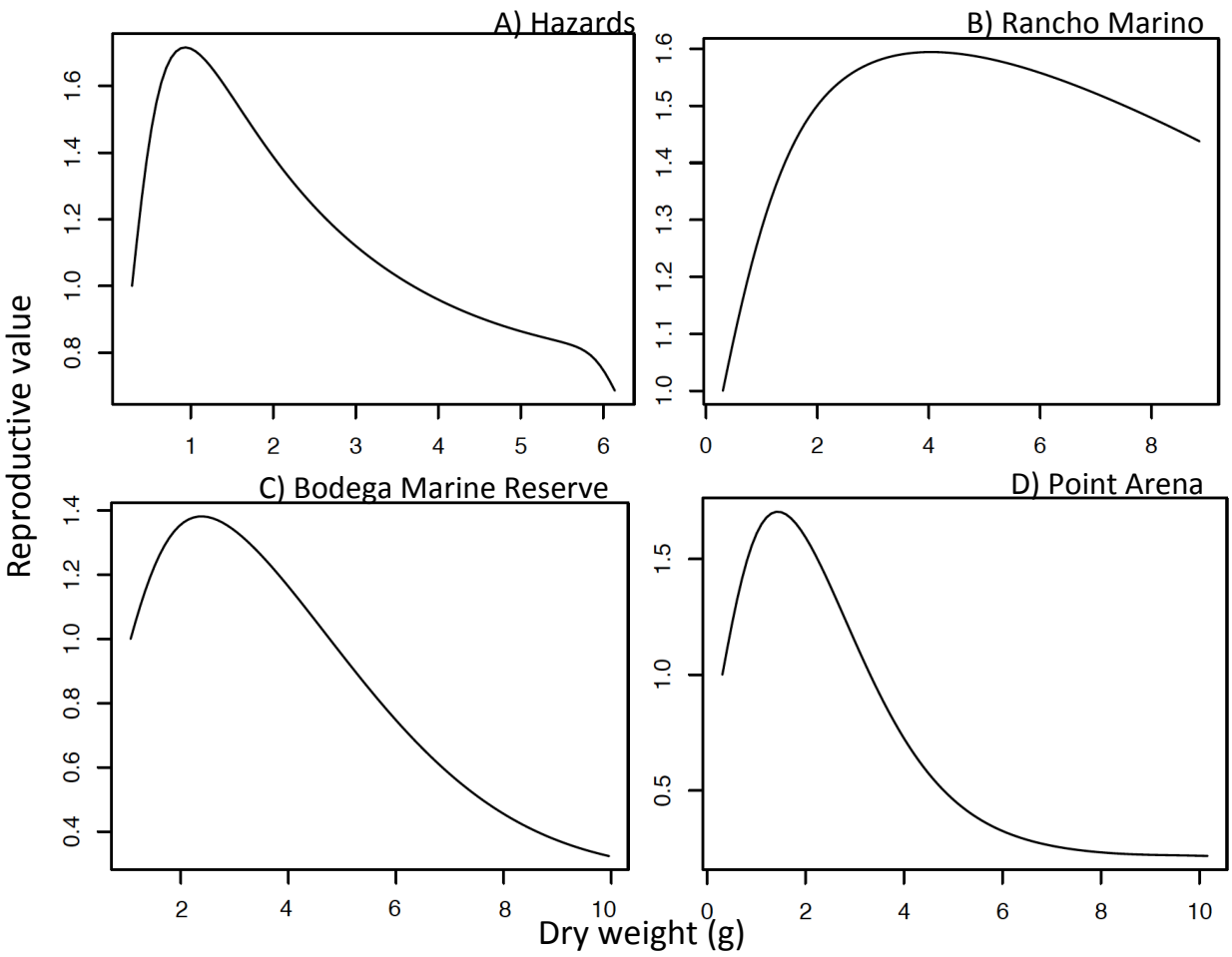

Figure 3.5 Relative reproductive value for the integral projection model of *Pelvetiopsis* at each site. The x- and y-axis scales are different among the panels.

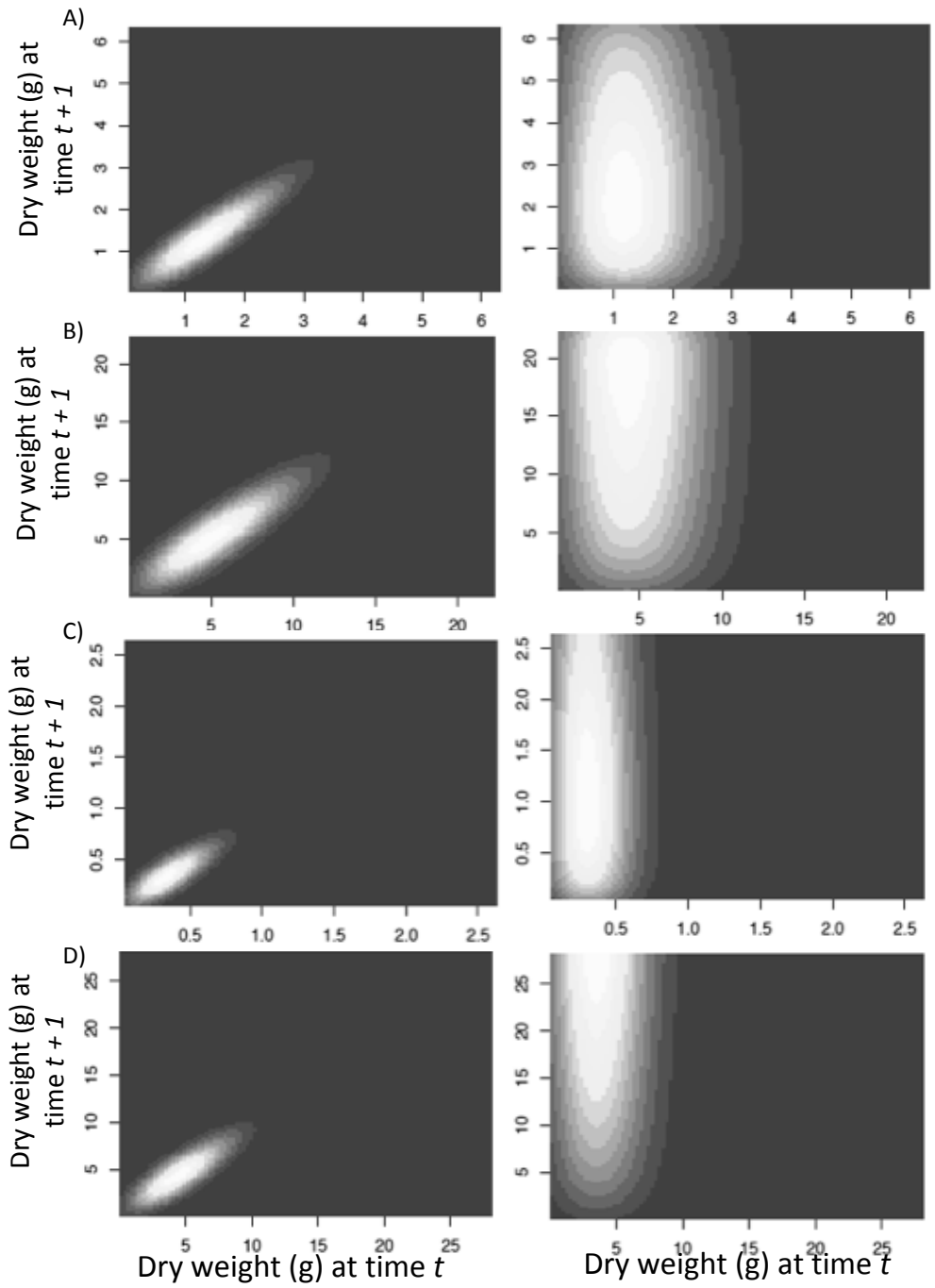

Figure 3.6 Elasticity and sensitivity for the integral projection mode for *Silvetia* at each site. A) Hazards B) Rancho Marino C) Bodega Marine Reserve D) Point Arena Lighter grey indicates a higher value The x- and y-axis scales are different among the panels.

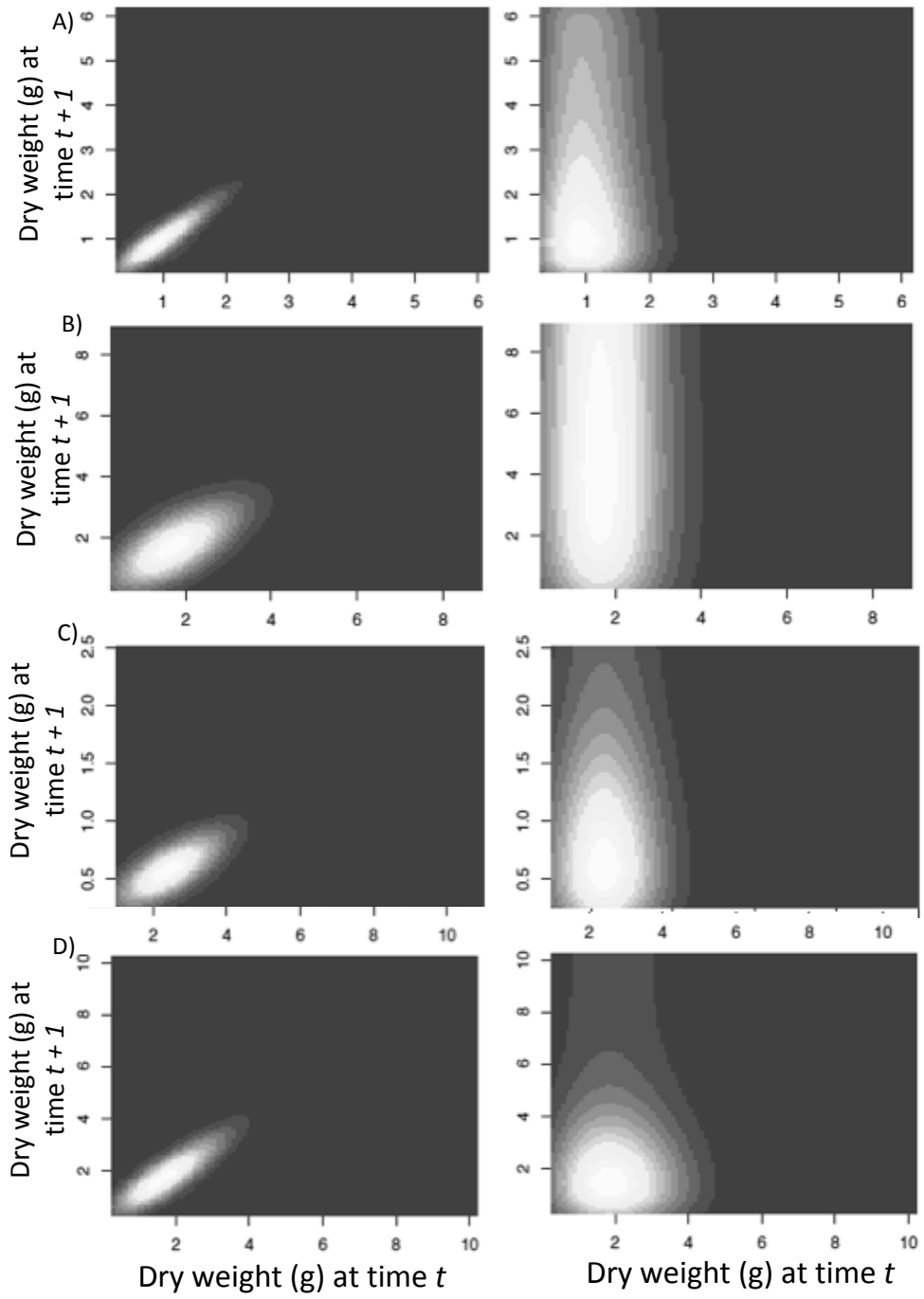

Figure 3.7 Elasticity and sensitivity for the integral projection mode for *Silvetia* at each site. A) Hazards B) Rancho Marino C) Bodega Marine Reserve D) Point Arena Lighter grey indicates a higher value The x- and y-axis scales are different among the panels.

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APPENDIX A

Table 1. Repeated-measures ANOVA of richness of mobile invertebrates in *Pelvetiopsis* plots Bodega Marine Reserve

Effect	DFn	DFd	Sum of Squares	F	p
Treatment	4	10	3.81	0.13	0.96
Month	4	40	10.75	1.37	0.24
Treatment* Month	16	40	13.39	0.43	0.97

Table 2. Repeated-measures ANOVA of abundance of mobile invertebrates in *Pelvetiopsis* plots Bodega Marine Reserve

Effect	DFn	DFd	Sum of Squares	F	p
Treatment	4	10	3.12	0.15	0.86
Month	4	40	8.74	1.41	0.28
Treatment* Month	16	40	14.77	0.55	0.87

Table 3. Repeated-measures ANOVA of richness of mobile invertebrates in *Pelvetiopsis* plots Rancho Marino

Effect	DFn	DFd	Sum of Squares	F	p
Treatment	4	10	35.86	0.62	0.66
Month	4	40	871.78	1.72	0.16
Treatment* Month	16	40	264.93	1.39	0.19

Table 4. Repeated-measures ANOVA of abundance of mobile invertebrates in *Pelvetiopsis* plots Rancho Marino

Effect	DFn	DFd	Sum of Squares	F	p
Treatment	4	10	2.88	0.12	0.97
Month	4	40	12.61	0.94	0.65
Treatment* Month	16	40	19.39	0.36	0.98

Table 5. Repeated-measures ANOVA of richness of mobile invertebrates in *Pelvetiopsis* plots Corona del Mar (p-values Greenhouse-Geisser corrected)

Effect	DFn	DFd	Sum of Squares	F	p
Treatment	4	10	79.92	13.26	7.34×10^{-4}
Month	4	40	10.98	1.88	0.01
Treatment* Month	16	40	17.14	0.74	0.04

Table 6. Repeated-measures ANOVA of abundance of mobile invertebrates in *Pelvetiopsis* plots Corona del Mar (p-values Greenhouse-Geisser corrected)

Effect	DFn	DFd	Sum of Squares	F	p
Treatment	4	10	2935.25	32.54	8.74×10^{-5}
Month	4	40	45.79	1.45	9.38×10^{-6}
Treatment* Month	16	40	474.61	3.76	5.66×10^{-5}

Table 7. Repeated-measures ANOVA of richness of mobile invertebrates in *Silvetia* plots Bodega Marine Reserve

Effect	DFn	DFd	Sum of Squares	F	p
Treatment	4	10	7.17	0.15	0.87
Month	4	40	30.55	1.45	0.64
Treatment* Month	16	40	18.99	0.78	0.76

Table 8. Repeated-measures ANOVA of abundance of mobile invertebrates in *Silvetia* plots Bodega Marine Reserve

Effect	DFn	DFd	Sum of Squares	F	p
Treatment	4	10	8.77	0.32	0.94
Month	4	40	6.14	2.19	0.43
Treatment* Month	16	40	18.97	0.63	0.85

Table 9. Repeated-measures ANOVA of richness of mobile invertebrates in *Silvetia* plots Rancho Marino

Effect	DFn	DFd	Sum of Squares	F	p
Treatment	4	10	55.99	0.75	0.81
Month	4	40	81.61	3.7	0.41
Treatment* Month	16	40	124.99	3.39	0.56

Table 10. Repeated-measures ANOVA of abundance of mobile invertebrates in *Silvetia* plots Rancho Marino

Effect	DFn	DFd	Sum of Squares	F	p
Treatment	4	10	4.76	0.65	0.71
Month	4	40	14.69	0.78	0.81
Treatment* Month	16	40	13.56	0.48	0.78

Table 11. Repeated-measures ANOVA of richness of mobile invertebrates in *Silvetia* plots Corona del Mar (p-values Greenhouse-Geisser corrected)

Effect	DFn	DFd	Sum of Squares	F	p
Treatment	4	10	136.61	6.40	9.14×10^{-6}
Month	4	40	5.54	0.34	3.99×10^{-4}
Treatment* Month	16	40	38.32	0.59	1.94×10^{-5}

Table 12. Repeated-measures ANOVA of abundance of mobile invertebrates in *Silvetia* plots Corona del Mar (p-values Greenhouse-Geisser corrected)

Effect	DFn	DFd	Sum of Squares	F	p
Treatment	4	10	186.11	8.64	8.04×10^{-4}
Month	4	40	7.74	1.39	8.74×10^{-5}
Treatment* Month	16	40	38.3	3.59	1.11×10^{-3}